FINE ROOT DYNAMICS IN THE BOREAL FOREST OF NORTHERN SASKATCHEWAN, CANADA

A Thesis Submitted to the College of Graduate Studies and Research

in Partial Fulfillment of the Requirements for

the Degree of Master's of Science

in the Department of Soil Science

University of Saskatchewan

Saskatoon, Canada

By

Shawn Alexander McDonald

PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying this thesis in any matter, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis in work or, in their absence, by the head of the Department or the Dean of the college in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Request for permission to copy or to make other use of materials in this thesis in whole or in part should be addressed to:

Head of the Department of Soil Science
University of Saskatchewan
51 Campus Drive
Saskatoon, Saskatchewan, Canada
S7N 5A8

ABSTRACT

The study of fine roots (FR) (roots < 2 mm in diameter) in the boreal forests has become a focus of many forest researchers in the past decade in an effort to better understand belowground processes and improve current carbon (C) models to better predict possible C sinks and sources. The objectives of this study were: 1) to determine the inter-annual variability in FR C production in relation to C cycling and other fluxes for four Saskatchewan boreal sites during a four year period, 2) to determine if minirhizotron (MR) estimates of root biomass were similar to root coring estimates, 3) to determine how root production, mortality, turnover, and longevity vary with root diameter class and soil depth, and 4) to determine if image collection orientation influenced estimates of FR biomass and production. Four Saskatchewan boreal sites including aspen (*Populus tremuloides*) (OA), black spruce (*Picea mariana*) (OBS), and two jack pine (*Pinus banksiana*) (mature – OJP, young – HJP94) stands were selected and MR were installed in July of 2002. Minirhizotron images were collected monthly from the end of May through September from 2003 to 2006. Total ecosystem C was estimated to be 47.5, 78.1, 163.1, and 450.5 Mg ha^{-1} for HJP94, OJP, OA, and OBS, respectively. The FR component of the ecosystem carbon storage ranged from 0.7 Mg ha^{-1} (1%) at HJP94 to 1.2 Mg ha^{-1} (< 1%) at OBS. Fine roots were found to contribute a very large portion of C production with estimates of 1.0, 0.6, 1.2, and 1.5 Mg ha^{-1} yr^{-1} accounting for 47, 27, 25, and 54% of total ecosystem C production at HJP94, OJP, OA, and OBS, respectively. In a one time comparison of MR and soil cores, FR biomass estimates were found to be similar at OJP, OA, and OBS, with MR estimates being significantly greater at HJP94. Approximately 85, 90, 96, and 96% of FR measured in this study were found to be less than 0.5 mm in diameter with median diameters of 0.250 ± 0.237, 0.225 ± 0.208, 0.175 ± 0.149 and 0.150 ± 0.149 (median ± SD) mm at HJP94, OJP, OA, and OBS, respectively. Fine root longevity was found to increase with increasing diameter and soil depth while turnover decreased. In many cases, it was found that even within a diameter interval of < 0.1 mm, differences in biomass, production, turnover, and longevity were detectable. This brings into question the use of the traditional 2 mm diameter class in FR studies. Fine root data, such as presented in this thesis, help to fill in some of the gaps in the knowledge base, enabling researchers to better understand the underground processes of the boreal forest and develop more complex and accurate C models.

ACKNOWLEDGEMENTS

I would like to begin by thanking my advisor, Dr. Ken Van Rees. Without his help and support this thesis would not have come to fruition. Ken made himself available not only in an academic capacity, but also a personal one. He taught me that learning truly does transcend the classroom and that the best way to learn is to get your hands dirty. That is a lesson that I try to apply to most facets of my life and I try to pass along the message every chance I get, whether it be in the classroom, the field, work, or at home.

I would also like to thank the members of my committee: Drs. Jeff Schoenau, Darwin Anderson, and Nicolas Bélanger and my external examiner, Dr. Jeff Thorpe. Their help and advice throughout this process was invaluable.

The field component of this study could not have been done without the help of a number of fantastic people: Doug Jackson, Bachitter Singh, Michael Steckler, Jeff Gunderson, Amber Jones, Melissa and Rachel Van Rees, Sheala Konecsni, and Christine Stadnyk. The many trips to northern Saskatchewan were made memorable by these individuals. My stay in the Department of Soil Science at the University of Saskatchewan brought me in contact with dozens of individuals that touched my life in one way or another and I am eternally grateful for their friendships. A special thank you is required for Heidi Lazorko. I never would have been able to make it this far without her. From late nights working on stats, long days in the field, and countless hours of talking, Heidi's moral support really helped me through some tough times. Without my friends to push me along and provide me with opportunities to take my mind off of things from time to time, I would have gone crazy. Thank you for the fun and the memories. You mean the world to me.

I have to thank my family most of all. Without their unwavering support and belief in me, I do not know where I would be. My parents, Murray and Marlene McDonald, endured many late night phone calls from a frustrated and stressed son. Their constant encouragement saw me through to the end of this project and beyond. There is no way that I could have completed this work without them. My sister Nicole and my grandparents, Ken and Lorna McDonald, were always there for me when I needed them and were always interested to hear about my work. The same goes for the rest of my extended family. Thank you all from the bottom of my heart.

Funding for this project was provided by the Fluxnet Canada research program.

DEDICATION

I would like to dedicate this thesis to my family for all of the love, support, and understanding they provided throughout this journey. Without them, this endeavor would not have been possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

1 INTRODUCTION

Global climate change has become a primary focus for many members of the scientific community over the past few years due to escalating greenhouse gas emissions. Anthropogenic carbon dioxide (CO_2) emissions to the atmosphere have been increasing exponentially since the beginning of the Industrial Revolution in the late 18^{th} and early 19^{th} centuries (Falkowski et al., 2000). Carbon dioxide is a common greenhouse gas and plays an important role as a carbon (C) source in photosynthesis (Bonan and Shugart, 1989). While not the most potent of the greenhouse gases, CO_2 is the greatest contributor to atmospheric warming through "positive radiative forcing" due to its high concentration in the atmosphere (Malhi et al., 2002). The two greatest CO_2 "sinks" in the C budget are the oceans and the terrestrial biosphere which can also be a C source under certain conditions such as land-use changes (Dixon et al., 1994; Falkowski et al., 2000; Malhi et al., 2002). With approximately 4.1 billion ha of the world's land surface covered by forests (Dixon et al., 1994), the importance of the Earth's forests in the global C cycle has been brought to the world's attention. The extent of the role forests play in the global C budget is still under investigation (Howard et al., 2004; Liu et al., 2005). Boreal forests comprise approximately 1.47 billion ha or 11% of the terrestrial surface area (Bonan and Shugart, 1989) and hold 49% of the global forest C pool totaling nearly 563.5 Gt of C (Dixon et al., 1994).

The boreal forests of the world are found in a circumpolar band in the northern latitudes stretching from the grasslands and temperate forests to the tundra. Boreal forests in Canada are generally comprised of mixed wood species including black spruce (*Picea mariana*), larch (*Larix laricina*), trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), and jack pine (*Pinus banksiana*). They are generally distributed along a moisture gradient from very wet or moist to dry (Malhi et al., 1999). Climate in boreal regions is subject to large seasonal fluctuations in moisture and temperature ranging from long, cold, dry winters to relatively short, warm, wet summers (Bonan and Shugart, 1989). Boreal forests contain on average 89.7 Mg C ha^{-1} in the vegetation with a further 208 Mg C ha^{-1} in the soils (Lal et al., 1997).

A great deal of knowledge has been accumulated about the aboveground components of forest systems, but little is understood about belowground processes. How much C is stored in the root systems of trees? How fast is the C accumulating and how long will it remain sequestered belowground? These are a few seemingly simple but

important questions that scientists around the world are attempting to answer. Approximately 3% of the belowground C pool in the boreal forest is located in tree and plant roots with the bulk of the belowground C content found in soil organic matter (calculated from Malhi et al. (1999)). Fine roots (roots < 2 mm in diameter) account for approximately 2.8 Mg ha^{-1} of biomass C in the boreal forest with coarse roots contributing around 8.0 Mg ha^{-1} (Gower et al., 1997; Steele et al., 1997). A better understanding of the dynamics of fine root (FR) production and turnover brings us one step closer to completing the Canadian and eventually the global C budget.

Complex models are often used to predict various outcomes of climate change (Jackson et al., 1996). These models require detailed estimates of various input parameters to maximize the effectiveness of their predictions. Studies of FR dynamics are difficult to do in a nondestructive manner. Roots are often excavated by hand with small tools, high pressure air or water but these are static measurements and do not reflect the dynamics of below ground C cycling by roots. As such, methods and tools such as minirhizotrons (MR), offer a nondestructive alternative to study FR and their role in C cycling and have gained in popularity in recent years. The use of MR enables researchers to estimate numerous root growth parameters such as biomass, production, longevity, and turnover *in situ*.

This project was completed in part with Fluxnet Canada and the Boreal Ecosystem Research and Monitoring Sites (BERMS) in northern Saskatchewan. Fluxnet Canada is a research network of Canadian scientists working together to measure various C fluxes in the boreal forest with the goal of building a better C budget. The primary objectives of this study were: 1) to determine the inter-annual variability in FR C production in relation to C cycling and other fluxes for four Saskatchewan boreal sites during a four year period, 2) to compare MR estimates of root biomass to root coring estimates, 3) to determine how root production, mortality, turnover, and longevity vary with root diameter class and soil depth, and 4) to determine if the sampling orientation of MR images influenced estimates of FR biomass and production.

There are six chapters in this thesis that attempt to answer a variety of questions about the growth of FR in the boreal forest of northern Saskatchewan. Chapter 2 is a review of literature related to boreal FR biomass, production, longevity, and turnover and the methodologies used to measure them. Also discussed are the environmental factors that may have an effect on FR growth.

Chapter 3 consists of several elements. The primary study component compares FR biomass and production estimates from 2003 to 2006 at four boreal sites including one aspen, one black spruce, and two jack pine stands. In another part of this study, FR

biomass estimates from MR data were compared to estimates from soil cores to help validate the use of the plane intersect method. The purpose of the final portion of this study was to relate MR FR biomass C and C production estimates to other boreal ecosystem components measured by other researchers.

Chapter 4 looks at the influence of root diameter class and soil depth on MR estimates of FR biomass, production, turnover, and longevity. For this study, a set of six diameter classes and two soil depth intervals were used to re-analyze MR data from Chapter 3.

Chapter 5 provides a comparison of MR image sampling orientations (top of tubes vs. sides) as well as a description of several tube excavations at each of the four research sites 4 years after installation.

Chapter 6 is a summary of the results of Chapters 3 to 5 and relates their significance to the greater field of FR research and suggestions on possible directions of future research to enhance the study of fine root dynamics.

1.1 Literature Cited

Bonan, G.B., and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst. 20:1.

Dixon, R.K., A.M. Solomon, S. Brown, R.A. Houghton, M.C. Trexier, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science 263:185-190.

Falkowski, P., R.J. Scholes, E. Boyle, J. Canadell, D. Canfield, J. Elser, N. Gruber, K. Hibbard, P. Hogberg, S. Linder, F.T. Mackenzie, B. Moore, III, T. Pedersen, Y. Rosenthal, S. Seitzinger, V. Smetacek, and W. Steffen. 2000. The global carbon cycle: a test of our knowledge of Earth as a system. Science 290:291-296.

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, and S.J. Steele. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102:29029-29041.

Howard, E.A., S.T. Gower, J.A. Foley, and C.J. Kucharik. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Glob. Change Biol. 10:1267-1284.

Jackson, R.B., J. Canadell, J.R. Ehleringer, H.A. Mooney, O.E. Sala, and E.D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411.

Lal, R., J. Kimble, and R. Follett. 1997. Land use and soil C pools in terrestrial ecosystems, p. 1 - 10, *In* Management of carbon sequestration in soil. CRC Press, Boca Raton, FL, USA.

Liu, J., D.T. Price, and J.M. Chen. 2005. Nitrogen controls on ecosystem carbon sequestration: a model implementation and application to Saskatchewan, Canada. Ecol. Model. 186:178-195.

Malhi, Y., D.D. Baldocch, and P.G. Jarvis. 1999. The carbon balance of tropical, temperate, and boreal forests. Plant Cell Environ. 22:715-740.

Malhi, Y., P. Meir, and S. Brown. 2002. Forests, carbon and global climate. Phil. Trans. R. Soc. Lond. A. 360:1567-91.

Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17:577-587.

2 LITERATURE REVIEW

2.1 Roots in the boreal forest

Roots are a complex and poorly understood physical link between plant and soil (Persson, 1983; Pregitzer, 2002; Zobel, 2003). Many soil characteristics such as horizonation, aggregation, and organic matter content are strongly influenced by the life processes of roots (Burke and Raynal, 1994; Fisher and Binkley, 2000; Gill and Jackson, 2000; Norby and Jackson, 2000; Silver and Miya, 2001). An understanding of the ecological mechanisms influenced by tree roots and root processes is becoming increasingly important in gaining a better understanding of global carbon (C) cycling (Brunner and Godbold, 2007; Majdi et al., 2007). In a study by Gill and Jackson (2000), fine root (FR) turnover was estimated to account for as much as one third of global net primary production.

In the Boreal Forest, the primary root forms include tap roots, heart roots, and flat roots which are common to jack pine, trembling aspen, and black spruce respectively (Figure 2.1) (Fisher and Binkley, 2000). The root's primary functions include structure and support as well as water and nutrient uptake (Fisher and Binkley, 2000; Smith and Smith, 2003). The tap roots and heart roots tend to extend deep into the mineral soil, while the flat root system is usually located in organic soil horizons with few vertical sinkers (Fitter, 1996). Jack pine tap roots enable the tree to access deep soil moisture in rapidly drained sandy soils, whereas the flat roots of black spruce tend to be very shallow due to a high water table and low-oxygen conditions (Fisher and Binkley, 2000; Strong and La Roi, 1983a). The majority of roots are located in the upper 1 m of the mineral soil with lateral roots extending horizontally in excess of 15 m in search of water and soil nutrients (Fisher and Binkley, 2000). The density of the roots is greatly controlled by soil properties such as soil moisture and temperature as well as tree genetics (Fisher and Binkley, 2000; Fitter, 1996).

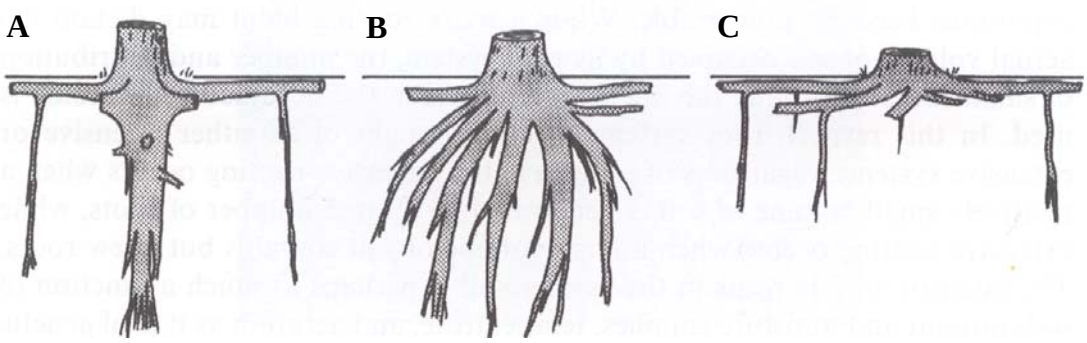

Figure 2.1: Schematic representation of common root systems found in the boreal forest including A) taproots (*Pinus banksiana*), B) heart roots (*Populus tremuloides*), and C) flat roots (*Picea mariana*) (Source: Fisher and Binkley, 2000)

Tree roots are often differentiated from one another by size, function, and morphology into coarse supportive roots, small-diameter woody roots, and FR (Bloomfield et al., 1996). An arbitrary diameter range of < 2 mm is commonly used in FR research. However, the definition of a FR varies widely among studies and can range from < 1 to 10 mm in diameter (Johnson et al., 2001; Kalyn, 2005; Li et al., 2003; Pregitzer, 1998; Steele et al., 1997; Wells and Eissenstat, 2001) These arbitrarily assigned diameter values reduce the complexity of root system data for easier analysis (Pregitzer, 2002). For the purposes of the studies discussed in this thesis, FR will be defined as all roots < 2 mm in diameter. Generalized FR diameter definitions make the assumption that all roots of that size class behave in a similar manner (Block et al., 2006; Satomura et al., 2007; Wells and Eissenstat, 2001; Zobel, 2003); however, studies have found that FR of different diameters within the 2 mm size definition have different physiologies, functionalities, and lifespans (Guo et al., 2007; Pregitzer, 2002; Pregitzer, 1998; Wells and Eissenstat, 2001). These topics will be discussed further in a later section of this paper.

2.2 Influence of the soil environment

The type and shape of a root system are highly dependent on the surrounding soil environment (Fisher and Binkley, 2000; Fitter, 1996; Glinski and Lipiec, 1990; McMichael and Quisenberry, 1993). Abiotic factors such as soil moisture, temperature and nutrient availability tend to have the greatest influence on FR dynamics. None of these factors work alone, but rather in intricate interactions with each other and other factors (Block et al., 2006; Glinski and Lipiec, 1990; McMichael and Quisenberry, 1993).

One of the primary factors affecting root structure is soil moisture. In dry soils, rooting depth and rooting density may increase while root elongation (horizontal spread) may be greatly reduced such as in xeric jack pine sites (McMichael and Quisenberry, 1993; Strong and La Roi, 1983a). Similarly, the low oxygen content of a saturated soil can greatly reduce the growth and function of newer metabolically active roots, while older less active roots can continue to respire until the oxygen concentration reaches approximately 10% (Drew and Stolzy, 1996). Shallow flat root systems such as those of black spruce are concentrated in the organic horizon of the forest soils in response to the high water table found at many sites (Strong and La Roi, 1983a; Strong and La Roi, 1983b). Water is also the medium by which many soil nutrients reach the root surface, and as such, the soil-water status has a direct impact on root-nutrient availability (McMichael and Quisenberry, 1993).

Soil temperature also has a large influence on FR dynamics (Côté et al., 1998; Noguchi et al., 2007; Pregitzer et al., 2000). Seasonal warming of the soil occurs from spring thaw to mid- to late-summer and then the soils begin to cool again. This fluctuation in temperature is responsible for controlling root growth and mortality along with initiation of lateral roots and root branching patterns (McMichael and Quisenberry, 1993; Pregitzer et al., 2000). Minimum soil temperatures for root growth are species dependent and range from 0 to 7 °C, with ideal conditions being between 10 to 25 °C and a maximum range of 25 to 35 °C (Fisher and Binkley, 2000; McMichael and Quisenberry, 1993; McMichael and Burke, 1996; Pregitzer et al., 2000). Steele et al. (1997) found that a peak in root elongation in a black spruce (*Picea mariana*) stand occurred later than at aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) stands. This was attributed to the insulating effect of the mossy understory at the black spruce site that delayed the warming of the soil compared to the aspen and jack pine sites with a comparatively thin forest floor. Temperature can also influence other environmental factors such as water and nutrient availability (Norby and Jackson, 2000). Higher temperatures result in increased nitrogen mineralization provided soil moisture does not limit microbial activity (McMichael and Burke, 1996; Pregitzer et al., 2000). Similarly, higher temperatures and moisture levels increase decomposition of detritus resulting in an increase in soil organic C (Li et al., 2003; Smucker, 1993).

Soil nutrient availability also has an effect on the rooting systems of boreal species. Root proliferation often occurs in zones of high nutrient availability (Fisher and Binkley, 2000; Pregitzer et al., 2002). Deficiencies in essential nutrients such as calcium (Ca) and nitrogen (N) can lead to developmental problems such as root stunting. Similarly, in a study of yellow birch (*Betula alleghaniensis)* in New Hampshire, US, roots were found to experience stunted growth due to aluminum (Al) toxicity. The degree of toxicity was influenced by the relative abundance of other nutrients such as magnesium (Mg) and sulfur (S). Tests done with Mg and S deficient media showed an 80% decrease in root growth with the addition of aluminum compared to the –Mg and –S treatment with no Al (Hoyle, 1971). Nitrogen (N) is often the limiting factor in plant-soil systems. Increased nitrate in the soil can positively affect lateral root production resulting in a proliferation of roots (McMichael and Quisenberry, 1993). However, excess N levels can also be detrimental to FR growth (Fisher and Binkley, 2000). Increases in soil N availability have been found to both increase and decrease FR lifespans in different studies (Burton et al., 2000). One suggestion for an increase in average lifespan with an increase in N availability proposed by Burton et al. (2000) is that the FR were maintained as long as the value of the nutrients they provide outweigh the C

cost of keeping them alive. Carbon cycling and ecosystem C:N ratios are controlled by the soil mineral N content. As N is often limiting, the benefits of increasing atmospheric carbon dioxide (CO_2) are also likely to be limited (King et al., 2005; Liu et al., 2005).

Fine root biomass and longevity estimates have been found to vary with depth, with the majority of FR being found in the upper 30 cm of the soil profile (Baddeley and Watson, 2005; Brunner and Godbold, 2007; Wells and Eissenstat, 2001). Jackson et al. (1996) reported that 83% of FR biomass in boreal forests was located in the upper 30 cm of soil. Kummerow et al. (1990) found that FR biomass decreased rapidly for all root diameter classes to a depth of 20 – 30 cm, with little change from 30 – 100 cm (Figure 2.2). Fine root longevity has been shown to be much greater for roots deeper in the soil profile as compared to those nearer the surface (Baddeley and Watson, 2005; Joslin et al., 2006; Wells and Eissenstat, 2001). Although a clear reason for this shift in longevity with depth is not presently known, it is believed to be linked to reduced fluctuations in soil moisture and temperature levels and perhaps reduced herbivory by soil fauna with depth.

A number of studies have found a significant relationship between root biomass and turnover with increasing CO_2 content (King et al., 2005; King et al., 2001; Pregitzer et al., 1995; Tingey et al., 2000). Pregitzer et al. (1995) found that while increased CO_2 coupled with available soil N resulted in an increase in root length growth, FR mortality doubled compared to ambient CO_2 levels. King et al. (2001) found that with an increase in CO_2 levels, FR biomass increased 96% accompanied with a 39% increase in soil respiration when compared to the control plots in aspen (*Populous tremuloides*) and mixed aspen and paper birch (*Betula papyrifera*) stands. The increase in atmospheric CO_2 associated with global climate change could have a large impact on boreal FR dynamics.

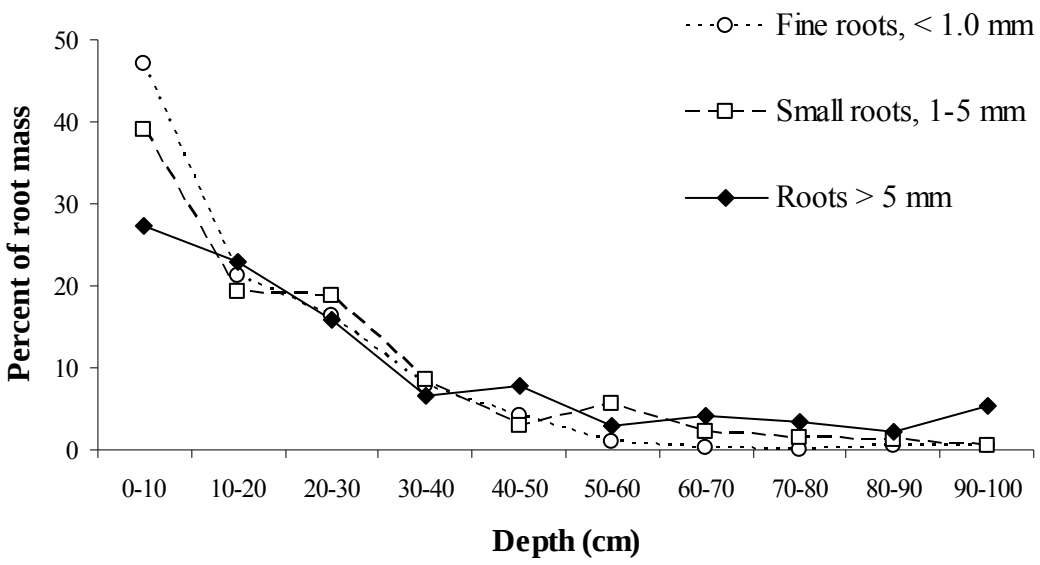

Figure 2.2: Percent root diameter distribution in 10 cm depth intervals for *Quercus coccifera* L., in Southern France. Values from 0 – 50 cm are means of 48 samples while values from 50-100 cm are means of 3 samples. (redrawn from Kummerow et al., 1990).

2.3 Methods of fine root measurement

Estimating FR processes and parameters can be difficult due to the high degree of variability associated with belowground root dynamics. There are two main types of methodologies for studying FR: destructive and non-destructive. Destructive methods such as root excavation or sequential soil coring allow for a one-time "snapshot" of the rooting system. Nondestructive methods such as minirhizotrons (MR) allow for repeated *in situ* root measurements (Cheng et al., 1991; Hendrick and Pregitzer, 1996a; Johnson et al., 2001; Vogt et al., 1998). Both methods can result in sampling error that can lead to the over- or under- estimation of FR production and mortality (Bernier and Robitaille, 2004).

2.3.1 Minirhizotrons

The use of MR in FR studies has gained popularity in recent years. As with most FR methods, MR studies are often tedious and time-consuming. Minirhizotrons also come with a large startup cost to buy the necessary equipment (Hendrick and Pregitzer, 1996a). A basic MR system consists of a number of clear acrylic, acrylate, or acetate-butyrate tubes inserted into the ground at an angle between 30 – 45º from the horizontal (Box, 1996). Angled installation of the tube (usually between 30 – 45^{o} from the horizontal) allows for root observation at a range of depths while reducing the chances of creating preferential rooting paths (Johnson et al., 2001; Smucker, 1993). Vertical tubes are avoided due to preferential water flow around the tube that can disrupt the tube-soil contact and can alter the rooting environment. Horizontal tubes can be used to observe roots at a single depth, but they are difficult to install without disturbing the soil (Johnson et al., 2001). Proper installation of the MR tubes generally results in little soil disturbance. Good contact between the MR tube and the soil is crucial as any air gaps could alter root growth patterns (Box, 1996; Johnson et al., 2001). After installation, the MR tubes are held in place with vertically placed rebar pins and zip-ties to ensure that the tubes are not easily disturbed during image collection or by snowpack. A waiting period is required after tube installation to allow for settling and reestablishment of damaged roots (Box, 1996; Johnson et al., 2001; Vogt et al., 1998). This period is often on the order of several months to over a year. Damaged roots are susceptible to a proliferation effect that can greatly inflate biomass and productivity estimates (Steele et al., 1997). A number of techniques have been used to view the roots next to the MR tubes. Older techniques included the use of periscopes, endoscopes, lighted mirrors, and fibre optics with cameras (Johnson et al., 2001; Samson and Sinclair, 1994). The most current

method uses a modified video camera attached to an indexed handle to record digital images of the same tube location at every sampling interval (Box, 1996; Hendrick and Pregitzer, 1996a; Johnson et al., 2001; Steele et al., 1997; Vogt et al., 1998).

The Plane Intersect method as proposed by Bernier and Robitaille (2004) allows for the indirect estimation of both biomass and productivity directly from MR data. One of the primary benefits of this method is that it relies solely on three of the most robust root characteristics available from MR data; root diameter, length, and date of appearance. The common issue with any method of FR analysis is determining if the values are under- or over-estimated (Vogt et al., 1998). Other methods typically involve an assumed "depth of field" value assigned to add a third dimension (W*L*D) to the two dimensional (W*L) MR output to estimate biomass and production values for a volume of soil. The depths used typically range from 1 – 3 mm (Bernier and Robitaille, 2004; Johnson et al., 2001).

2.3.2 Soil cores

Sequential soil coring (SSC) has traditionally been the primary method used in FR analysis. However, it is labor intensive and lab analysis is long and tedious. Soil cores are most often collected using a known volume auger and sampling to a specified depth (Samson and Sinclair, 1994; Vogt and Persson, 1991). The soil cores are washed to separate the soil and debris from the roots which are then collected. The roots are often separated into arbitrary diameter classes that are dependent on the goals of the study. From the collected roots, estimates of root length, biomass, net primary productivity (NPP), and root nutrient contents can be made (Konôpka et al., 2005; Newman, 1966; Samson and Sinclair, 1994; Tennant, 1975). Parameters such as mortality, longevity, and turnover are difficult to determine with soil coring due to the impossibility of determining the date of root birth or death and the inherent spatial variability of rooting density (Hendrick and Pregitzer, 1992; Samson and Sinclair, 1994; Vogt et al., 1998). The key assumption in many studies concerning root production and/or mortality is that these two processes do not occur simultaneously. It is also difficult to accurately determine whether a root is living or dead (Bloomfield et al., 1996). The differentiation between living and dead roots requires a trained eye and possibly the use of dyes or physical tests such as brittleness (Vogt and Persson, 1991). Biomass, production, and longevity studies are often based on root dry weight, length or root counts (Kalyn, 2005). Root dry weight is simply measured after the washed root samples are oven-dried for a period of one to several days. Parameters such as root length density (RLD) are estimated using specialized scanning software (Farrell et al., 1993; Volkmar, 1993; Zutter, 1999) or

manually using a method such as Newman's line intercept method (Ephrath et al., 1999; Farrell et al., 1993; Kumar et al., 1993; Newman, 1966; Tennant, 1975).

2.4 Fine root analysis

Regardless of whether a study employs the use of MR or soil cores, a large amount of data concerning the temporal growth patterns, productivity, biomass, longevity/turnover rates, density, and depth distribution of FR is gathered. Data on all aspects of root dynamics are necessary for increasing our knowledge of the below-ground processes that occur in forests throughout the world.

2.4.1 Fine root morphology and temporal dynamics

In FR studies, there are generally three morphological stages identified: white, brown, and black. These three stages are used in MR studies to identify the growth stages of FR. New roots first appear white and with time begin to brown. Brown roots, while not necessarily woody, are generally considered to be alive and healthy but have experienced a senescence of the root cortex (Wells and Eissenstat, 2001; Wells and Eissenstat, 2003). Hendrick and Pregitzer (1992) found that root browning was accelerated with low soil water availability and high soil temperatures. Secondary growth during the brown phase of root production is monitored and accounted for during the MR image analysis. As roots transition from brown to black, they are considered to be dead or dying (Block et al., 2006; Hendrick and Pregitzer, 1992). This category can sometimes become deceiving as some black roots have been noted to produce new roots (author's personal observation). For this reason, a root is not removed from the analysis until the root decomposes completely or simply disappears from view (Kern et al., 2004; West et al., 2004). Differentiation among roots of varying species in a natural setting is difficult and often not possible in MR studies (Kalyn, 2005).

Many studies have found that there is a distinct seasonal pattern for FR growth (Bernier and Robitaille, 2004; Burton et al., 2000; Côté et al., 1998; Hendricks et al., 2006; Joslin et al., 2006; Kalyn, 2005; Wells and Eissenstat, 2001; Wells et al., 2002). Most studies describe a large flush of new FR in the spring as the soil begins to thaw. This large spike in FR production is usually followed by a gradual decline in productivity and biomass due to increased mortality over the course of the growing season. Decreased root numbers in the fall generally remain low throughout the winter months (Wells et al., 2002). Low rates of production during the late fall and winter months are typically related to soil temperatures that are below the threshold required for root growth as well as a decreased demand for water and nutrients (Hendrick and Pregitzer, 1996b;

McMichael and Burke, 1996; Pregitzer et al., 2000). It should also be noted that studies have also reported a bimodal FR growth pattern with high growth levels in the spring as well as in the fall (Kummerow et al., 1990; Wells and Eissenstat, 2003). This bimodal pattern was attributed to high moisture and temperatures late in the fall, producing a second flush of roots. Spring flushes of FR generally coincide with bud-break and leaf-out, but the timing of root production in relation to aboveground events is poorly understood in most forest types (Hendrick and Pregitzer, 1996b). Hendrick and Pregitzer (1996b) also suggested that trees in seasonal climates that are subject to mid-season droughts have adapted to take advantage of early-season soil moisture with a large flush of FR in the spring.

2.4.2 Fine root biomass and productivity

Biomass and productivity are among the most common FR parameters sought after in root studies. Both of these components are critical in the synthesis of a forest C budget and an understanding of biogeochemical dynamics (Cairns et al., 1997). Biomass is defined as a measurement of the standing crop of FR at a given time and space. Productivity is simply the change in biomass between two periods of time (Bernier and Robitaille, 2004). Collecting data on FR biomass and productivity is difficult and measurements are often highly variable. Biomass values have been estimated for numerous forest systems in the past using soil coring methods. However, the MR method is becoming increasingly popular and is making FR studies easier.

Many studies suggest that coarse woody root biomass is allometrically related to total aboveground biomass (Cairns et al., 1997; Li et al., 2003; Steele et al., 1997). Cairns et al. (1997) found that up to 84% of belowground biomass could be related to measures of aboveground productivity. With further study, a better understanding of total belowground root C allocation in comparison to that of the aboveground fraction can be gained (Cairns et al., 1997; Li et al., 2003).

Fine root biomass tends to fluctuate for a given site during the growing season as well as between growing seasons. Intra-annual variation in site biomass is generally represented by a large biomass value in the spring to summer that slowly decreases over late summer through fall within the same growing season. Fine root productivity follows a similar pattern with a spike early in the growing season and then decreasing through fall. It is important to remember that growth, mortality, and decay occur simultaneously, but are not necessarily constant through time (Hendrick and Pregitzer, 1993; Li et al., 2003; Santantonio and Grace, 1987; Steele et al., 1997; Vogt et al., 1998). Failure to take this into account can result in an underestimation of annual belowground biomass (Vogt

et al., 1998). The belowground ebb and flow of FR biomass often echoes that of the aboveground leaf production and senescence (Burke and Raynal, 1994) and is related to growing conditions (Steele et al., 1997).

Biomass estimates can vary greatly between studies due to differences in species, location, and sampling method (Table 2.1). Fine root biomass was found to be 0.43, 1.68, and 1.33 Mg ha^{-1} for trembling aspen, jack pine, and black spruce, respectively by Steele et al. (1997). In a review of root dynamics in various forest ecosystems by Vogt et al. (1996), FR biomass in the boreal forest was found to be approximately 1.3 Mg ha^{-1} (10% of total root biomass) for the broadleaf deciduous component and 0.6 to 1.65 Mg ha^{-1} (1 – 2% of total root biomass) for evergreens. Fogel (1983) stated in their review that FR biomass estimates for Douglas-fir (*Pseudotsuga menziesii*) ranged from 1 to 12.6 Mg ha^{-1} with an average of 5 Mg ha^{-1}. A review of research on Japanese temperate forests found that FR biomass ranged from 0.49 to 7.5 Mg ha^{-1}, depending on species (Noguchi et al., 2007). Jackson et al. (1996) reported an average standing root biomass value of 29 Mg ha^{-1} for coarse and FR in a review of boreal forest studies.

Net primary productivity (NPP) is the amount of biomass production after respiration has been accounted for, and is generally reported on a per year basis. In the boreal forest, FR NPP follows an inter-annual cycle with a peak in the spring to early summer and little to no production during the winter months (Fogel, 1983; Gower et al., 1997; Hendrick and Pregitzer, 1993; Steele et al., 1997). Steele et al. (1997) reported NPP values of 0.58, 2.35 and 2.09 Mg ha^{-1} yr^{-1} for mature aspen, black spruce, and jack pine, respectively. Other NPP values for boreal species can be found in Table 2.1.

Table 2.1: Reported values of annual fine root biomass and net primary production (NPP) for deciduous and coniferous forests in North America. (Adapted from Kalyn, 2005).

Dominant Species	Location	Root Collection Method	Root Diameter (mm)	Root Biomass (Mg ha^{-1})	Root NPP (Mg ha^{-1} yr^{-1})	Reference
Deciduous						
Acer saccharum	Michigan, USA	MR †	< 3	3.23	6.50	Aber et al. 1985
Acer saccharum	Michigan, USA	MR	< 2	6.88	7.30	Hendrick and Pregitzer 1993
Acer saccharum	New York, USA	MR	< 3	2.51	2.45	Coleman et al. 2000
Betula papyrifera	Alaska, USA	SC ‡	< 2	8.32	2.76	Ruess et al. 1996
Broadleaf deciduous	Compiled world data	MR	< 2	1.29	2.38	Vogt et al. 1996
Mixed hardwood	Quebec, CA	MR	< 2	--	2.51	Bernier and Robataille 2004
Populus balsamifera	Alaska, USA	SC	< 2	4.72	3.55	Ruess et al. 1996
Populus balsamifera	Alaska, USA	SC	< 2	4.69	4.39	Ruess et al. 1996
Populus tremuloides	Saskatchewan, CA	SC	< 5	6.57	0.73 §	Steele et al. 1997
Populus tremuloides	Saskatchewan, CA	MR	< 2	0.43	0.58	Steele et al. 1997
Populus tremuloides	Manitoba, CA	MR	< 2	0.66	0.88	Steele et al. 1997
Populus tremuloides	Wisconsin, USA	SC	< 1	1.32		King et al. 2001
Deciduous, average				3.93	3.09	
Coniferous						
Picea glauca	Alaska, USA	SC	< 2	3.05	1.57	Ruess et al. 1996
Picea glauca	Alaska, USA	SC	< 2	2.88	2.48	Ruess et al. 1996
Picea mariana	Alaska, USA	SC	< 2	2.20	2.32	Ruess et al. 1996
Needleleaf evergreen	Compiled world data	MR	< 2	1.03	0.60	Vogt et al. 1996
Picea mariana	Alaksa, USA	MR	< 2		2.28	Ruess et al. 2003
Picea mariana	Saskatchewan, CA	MR	< 1.5		2.22	O'Connell et al. 2003
Picea mariana	Manitoba, CA	MR	< 2	1.75	1.74	Steele et al. 1997
Picea mariana	Saskatchewan, CA	MR	< 2	1.33	2.35	Steele et al. 1997
Picea mariana	Saskatchewan, CA	SC	< 5	5.91	0.66	Steele et al. 1997
Pinus banksiana	Manitoba, CA	MR	< 2	1.33	1.90	Steele et al. 1997
Pinus banksiana	Saskatchewan, CA	MR	< 2	1.68	2.09	Steele et al. 1997
Pinus banksiana	Saskatchewan, CA	SC	< 5	2.86	0.24 §	Steele et al. 1997
Pinus contorta	British Columbia, CA	SC	< 5	6.40	4.90	Comeau and Kimmins 1989
Pinus contorta	British Columbia, CA	SC	< 5	4.30	4.70	Comeau and Kimmins 1989
Pinus palustris	Georgia, USA	MR	< 2	4.10		Jones et al. 2003
Pinus sylvestris	Central Sweden	SC	< 2	1.23		Persson, 2003
Coniferous, average				2.86	2.15	

† Minirhizotron observation.
‡ Soil core extraction.
§ Ingrowth core (fine root diameter < 2 mm).

2.4.3 Diameter class distribution

Knowledge of FR physiology and behavior has increased greatly over the past decade. In the past, there has been no distinction between roots of varying diameters within the broad definition of a FR (Vogt and Persson, 1991; Zobel, 2003). As mentioned above, the definition of a FR varies widely from study to study, ranging from 0.5 – 10 mm in diameter with 2 mm being the most common maximum diameter. Recently, a number of studies have attempted to prove that these large single diameter classes potentially mask the contributions of the smallest roots sampled toward turnover estimates as well as biomass and productivity values (Baddeley and Watson, 2005; Joslin et al., 2006; Pregitzer, 1998; Wells and Eissenstat, 2001). Guo et al. (2007) and Pregitzer et al. (2002) proposed choosing a narrow FR diameter class range such as 0 – 0.5 mm rather than 0 – 2 mm could help "reduce the heterogeneity in a root sample and improve the accuracy of turnover estimates". Pregitzer et al. (2002) reported that for eight of nine North American species surveyed by excavating intact root segments, 75% of the total root length was comprised of roots <0.5 mm in diameter. Baddely and Watson (2005) suggested that further subdivision of a 2 mm diameter class could be quite fruitful in future FR studies. Pregitzer (2002) summarized a number of articles concluding that the physiology and lifespan of individual roots may vary with "soil nutrient status, degree of mycorrhizal infection, and the position of a root on the branching root system" and that using broad arbitrary diameter classes for cross-species comparisons without considering FR form and function was "naïve".

It has been observed that there are differences in C:N ratios and respiration rates between roots of different diameters with the greatest metabolic activity occurring in the smallest diameter roots (Pregitzer et al., 1997; Pregitzer, 1998; Wells and Eissenstat, 2001). White metabolically active roots have been found to have greater C and N concentrations than brown or woody roots (Goldfarb et al., 1990; Pregitzer et al., 2002). Studies have found that N concentrations and root respiration rates vary in accordance with branching position and diameter (Fitter, 1996; Pregitzer, 1998). Wells and Eissenstat (2001) found in a study of apple (*Malus* domestica) in Pennsylvania that FR have a great deal of plasticity and adapt readily to their environment and the demands of the tree. Cahn et al. (1989) found that the daily rate of root elongation increased with increasing root diameter in maize. In a study of scrub oak (*Quercus coccifera*) in southern France, Kumerrow et al. (1990) found that at shallow soil depths where root biomass is greatest, FR <1 mm contributed the most to total root mass. Roots >5 mm contributed the most to biomass at greater depths in the same study. A number of studies

have found that FR generally have a greater turnover rate (lower longevity) than coarser, woody roots (Baddeley and Watson, 2005; Wells and Eissenstat, 2001). As some smaller arbitrary diameter classes may not work equally well for all species (Pregitzer, 2002), Guo et al. (2007) suggested that root order based classes may work better than classes based on diameter, but more development of this method is required. Zobel (2003) suggested that a root system should be thought of as an "integration of multiple genetically and anatomically determined functional root classes.

2.4.4 Root longevity and turnover

Longevity and turnover are critical factors to understand C cycling in FR (Steele et al., 1997). However, accurately measuring FR mortality directly is very difficult, making longevity and turnover estimates problematic (Bernier and Robitaille, 2004). Wells and Eissenstat (2001) used cohort analysis to estimate root longevity. A cohort is a group of roots whose mean date of appearance is known (the mean date is often the date halfway between sampling times). Cohorts of roots are often followed until the median lifespan is determined. The median lifespan is the length of time that it takes to achieve 50% cohort mortality. Median lifespan is often used as studies are rarely long enough to ensure 100% mortality within a cohort of roots. Roots that are not dead at the end of a study are considered "right-censored" and are not included in longevity calculations. The Kaplan-Meier (1958) nonparametric survivorship function is often used to calculate weighted longevity values (Majdi and Andersson, 2005).

Small diameter roots often appear and senesce rapidly; however, some studies reported that some tree FR can live for several years (Eissenstat et al., 2000; Tierney and Fahey, 2001). The exact mechanisms involved in root senescence are not clear, but it is generally believed to be related to environmental stresses and possibly hormonal signals from the tree itself (Schoettle and Fahey, 1994). Increased turnover rates have been related to elevated soil temperatures (Gill and Jackson, 2000). Depending on the diameter of the roots dying, the resulting degree of turnover could vary greatly (Fitter, 1996; Hendrick and Pregitzer, 1992). For example, a number of small roots < 0.5 mm in diameter could die with little consequence; however, if a larger root > 5 mm dies, a large number of smaller laterals could die with it, resulting in a much higher C cost to the tree (Pregitzer et al., 1997). Wells and Eissenstat (2001) noted that over-winter survivorship was greater for apple roots > 0.5 mm, while roots < 0.3 mm in diameter were unlikely to survive.

Wells and Eissenstat (2001) found that the median lifespan of apple FR to range from 36 – 114 days, whereas Hendrick and Pregitzer (1996) reported values of

approximately 240 days and 165 days for roots from 0 – 30 and 30 – 60 cm depths, respectively. Several studies suggest that root longevity generally increases with root diameter and coniferous species having greater FR longevity than deciduous trees (Bloomfield et al., 1996; Gill and Jackson, 2000; Tierney and Fahey, 2001; Wells and Eissenstat, 2001). Baddely and Watson (2005) reported median lifespans of 71 d for roots <0.2 mm versus 289 d for roots >0.5 mm for wild cherry (*Prunus avium*). As mentioned above, FR longevity was also found to vary with depth, with roots deeper in the soil profile surviving longer than those nearer the surface (Baddeley and Watson, 2005; Wells and Eissenstat, 2001). Mycorrhizal infections can also have a large impact on FR longevity. King et al. (2002) reported that roots with ectomycorrhizae had longer lifespans and lower turnover rates compare to non-mycorrhizal FR. However, Hooker et al. (1995) found that FR longevity decreased for *Populus generosa inter americana* when roots were colonized by mycorrhizae. Root survivorship also differs by cohort, so analysis should include several cohorts to minimize variance (Tierney and Fahey, 2001).

Fine root turnover is the process by which roots die and are replaced with a new standing crop of roots. Soil environmental factors such as soil temperature, moisture, and fertility have been considered to influence turnover rates (Bloomfield et al., 1996; Gill and Jackson, 2000). Turnover (yr^{-1}) is the inverse of the median cohort lifespan or longevity (yr) (Burton et al., 2000; Tierney and Fahey, 2001). Estimates of FR turnover can be calculated directly using: (1) the ratio of annual root length produced to average live root length observed; (2) the ratio of annual root length mortality to average live root length observed; and (3) the average of the above two measures (Burton et al., 2000). A theoretical turnover rate of 1.0 yr^{-1} would represent the death of all roots produced by a plant within a single growing season (Steele et al., 1997). Kalyn (2005) found average turnover rates of 0.85, 1.18, and 0.89 for mature black spruce, aspen, and jack pine stands, respectively and 0.73 yr^{-1} for a juvenile jack pine stand. Turnover rates for *Populus spp*. ranged from 0.5 yr^{-1} (Coleman et al., 2000) to 1.8 yr^{-1} (Steele et al., 1997) while turnover for *Acer saccharum* ranged from 0.4 – 0.8 yr^{-1} (Fogel, 1983; Hendrick and Pregitzer, 1993).

2.5 Literature cited

Baddeley, J., and C. Watson. 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant Soil 276:15-22.

Bernier, P.Y., and G. Robitaille. 2004. A plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265:165-173.

Block, R., K. Van Rees, and J. Knight. 2006. A review of fine root dynamics in *Populus* plantations. Agrofor. Syst. 67:73-84.

Bloomfield, J., K. Vogt, and P.M. Wargo. 1996. Tree turnover and senescence, p. 363-381, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half., 2nd ed. Marcel Dekker Inc, New York, New York, USA.

Box, J.J.E. 1996. Modern methods for root investigation, p. 193-237, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half. 2nd ed. Marcel Dekker Inc., New York, NY, USA.

Brunner, I., and D.L. Godbold. 2007. Tree roots in a changing world. J. For. Res. 12:78-82.

Burke, M.K., and D.J. Raynal. 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135-146.

Burton, A.J., K.S. Pregitzer, and R.L. Hendrick. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia 125:389-399.

Cahn, M., R. Zobel, and D. Bouldin. 1989. Relationship between root elongation rate and diameter and duration of growth of lateral roots of maize. Plant Soil 119:271-279.

Cairns, M.A., S. Brown, E.H. Helmer, and G.A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia 111:1-11.

Cheng, W., D.C. Coleman, and J.J.E. Box. 1991. Measuring root turnover using the minirhizotron technique. Agri. Ecosys. Environ. 34:261-267.

Coleman, M.D., R.E. Dickson, and J.G. Isebrands. 2000. Contrasting fine-root production, survival and soil CO_2 efflux in pine and polar plantations. Plant Soil 225:129-139.

Côté, B., W.H. Hendershot, J.W. Fyles, A.G. Roy, R. Bradley, P.M. Biron, and F. Courchesne. 1998. The phenology of fine root growth in a maple-dominated ecosystem: relationships with some soil properties. Plant Soil 201:59-69.

Drew, M.C., and L.H. Stolzy. 1996. Growth under oxygen stress, p. 363-381, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half. 2nd ed. Marcel Dekker Inc., New York, NY, USA.

Eissenstat, D.M., C.E. Wells, R.D. Yanai, and J.L. Whitbeck. 2000. Building roots in a changing environment: implications for root longevity. New Phytol. 147:33-42.

Ephrath, J.E., M. Silberbush, and P.R. Berliner. 1999. Calibration of minirhizotron readings against root length density data obtained from soil cores. Plant Soil 209:201-208.

Farrell, R.E., F.L. Walley, A.P. Lukey, and J.J. Germida. 1993. Manual and digital line-intercept methods of measuring root length: a comparison. Agron. J. 85:1233-1237.

Fisher, R.F., and D. Binkley. 2000. Ecology and Management of Forest Soils. 3rd ed. John Wiley & Sons, Inc., New York, NY, USA.

Fitter, A. 1996. Characteristics and functions of root systems, p. 1-20, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half. 2nd ed. Marcel Dekker Inc., New York, NY, USA.

Fogel, R. 1983. Root turnover and productivity of coniferous forests. Plant Soil 71:75-85.

Gill, R.A., and R.B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147:13-31.

Glinski, J., and J. Lipiec. 1990. Soil physical conditions and plant roots CRC Press, Inc., Boca Raton, FL, USA.

Goldfarb, D., R. Hendrick, and K. Pregitzer. 1990. Seasonal nitrogen and carbon concentrations in white, brown and woody fine roots of sugar maple (*Acer saccharum* Marsh). Plant Soil 126:144-148.

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, and S.J. Steele. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102:29,029-29,041.

Guo, D., H. Li, R.J. Mitchell, W. Han, J.J. Hendricks, T.J. Fahey, and R.L. Hendrick. 2007. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. New Phytol. 177:443-456.

Hendrick, R.L., and K.S. Pregitzer. 1992. The demography of fine roots in a northern hardwood forest. Ecology 73:1094-1104.

Hendrick, R.L., and K.S. Pregitzer. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Can. J. For. Res. 23:2507-2520.

Hendrick, R., and K.S. Pregitzer. 1996a. Applications of minirhizotrons to understand root function in forests and other natural ecosystems. Plant Soil 185:293-304.

Hendrick, R.L., and K.S. Pregitzer. 1996b. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. J. Ecol. 84:167-176.

Hendricks, J.J., R.L. Hendrick, C.A. Wilson, R.J. Mitchell, S.D. Pecot, and D. Guo. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J. Ecol. 94:40-57.

Hooker, J.E., K.E. Black, R.L. Perry, and D. Atkinson. 1995. Arbuscular mycorrhizal fungi induced alteration to root longevity of poplar. Plant Soil 172:327-329.

Hoyle, M.C. 1971. Effects of the chemical environment on yellow birch root development and top-growth. Plant Soil 35:623-633.

Jackson, R.B., J. Canadell, J.R. Ehleringer, H.A. Mooney, O.E. Sala, and E.D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411.

Johnson, M.G., D.T. Tingey, D.L. Phillips, and M.J. Storm. 2001. Advancing fine root research with minirhizotrons. Env. Exp. Bot. 45:263-289.

Joslin, J.D., J.B. Gaudinski, M.S. Torn, W.J. Riley, and P.J. Hanson. 2006. Fine-root turnover patterns and their relationship to root diameter and soil depth in a 14C-labeled hardwood forest. New Phytol. 172:523-535.

Kalyn, A. 2005. Fine root dynamics and belowground carbon-cycling in the boreal forests of Saskatchewan., University of Saskatchewan, Saskatoon, SK, Canada.

Kaplan, E.L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53:457-481.

Kern, C.C., A.L. Friend, J.M.-F. Johnson, and M.D. Coleman. 2004. Fine root dynamics in a developing *Populus deltoides* plantation. Tree Physiol. 24:651-660.

King, J.S., K.S. Pregitzer, D.R. Zak, W.E. Holmes, and K. Schmidt. 2005. Fine root chemistry and decomposition in model communities of north-temperate tree species show little response to elevated atmospheric CO_2 and varying soil resource availability. Oecologia 146:318-328.

King, J.S., T.J. Albaugh, H.L. Allen, M. Buford, B.R. Strain, and P. Dougherty. 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154:389-398.

King, J.S., K.S. Pregitzer, D.R.Zak, J. Sober, J.G. Isebrands, R.E. Dickson, G.R. Hendrey, and D.F. Karnosky. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. Oecologia 128:237-250.

Konôpka, B., J. Yuste, I. Janssens, and R. Ceulemans. 2005. Comparison of fine root dynamics in scots pine and pedunculate oak in sandy soil. Plant Soil 276:33-45.

Kumar, K., S.S. Prihar, and P.R. Gajri. 1993. Determination of root distribution of wheat by auger sampling. Plant Soil 149:245-253.

Kummerow, J., M. Kummerow, and L. Trabaud. 1990. Root biomass, root distribution and the fine-root growth dynamics of Quercus coccifera L. in the garrigue of southern France. Plant Ecol. 87:37-44.

Li, Z., W.A. Kurz, M.J. Apps, and S.J. Beukema. 2003. Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Can. J. For. Res. 33:126-136.

Liu, J., D.T. Price, and J.M. Chen. 2005. Nitrogen controls on ecosystem carbon sequestration: a model implementation and application to Saskatchewan, Canada. Ecol. Model. 186:178-195.

Majdi, H., and P. Andersson. 2005. Fine root production and turnover in a Norway spruce stand in northern Sweden: effects of nitrogen and water manipulation. Ecosystems 8:191-199.

Majdi, H., J.-E. Nylund, and G. Ågren. 2007. Root respiration data and minirhizotron observations conflict with root turnover estimates from sequential soil coring. Scand. J. For. Res. 22:299-303.

McMichael, B.L., and J.E. Quisenberry. 1993. The impact of the soil environment on the growth of root systems. Env. Exp. Bot. 33:53-61.

McMichael, B.L., and J.J. Burke. 1996. Temperature effects on root growth, p. 383-396, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half. 2nd ed. Marcel Dekker Inc., New York, NY, USA.

Newman, E.I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3:139.

Noguchi, K., B. Konôpka, T. Satomura, S. Kaneko, and M. Takahashi. 2007. Biomass and production of fine roots in Japanese forests. J. For. Res. 12:83-95.

Norby, R.J., and R.B. Jackson. 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol. 147:3-12.

Persson, H. 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil 71:87-101.

Pregitzer, K.S. 2002. Fine roots of trees - a new perspective. New Phytol. 154:267-270.

Pregitzer, K.S., M.E. Kubiske, C.K. Yu, and R.L. Hendrick. 1997. Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia 111:302-308.

Pregitzer, K.S., J.S. King, A.J. Burton, and S.E. Brown. 2000. Responses of tree fine roots to temperature. New Phytol. 147:105-115.

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, and C.S. Vogel. 1995. Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytol. 129:579-585.

Pregitzer, K.S., J.L. DeForest, A.J. Burton, M.F. Allen, R.W. Ruess, and R.L. Hendrick. 2002. Fine root architecture of nine North American trees. Ecol. Monogr. 72:293-309.

Pregitzer, K.S., M.J. Laskowski, A.J. Burton, V.C. Lessard, D.R. Zak. 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol. 18:665-670.

Samson, B.K., and T.R. Sinclair. 1994. Soil core and minirhizotron comparison for the determination of root length density. Plant Soil 161:225-232.

Santantonio, D., and J.C. Grace. 1987. Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Can. J. For. Res. 17:900-908.

Satomura, T., K. Fukuzawa, and T. Horikoshi. 2007. Considerations in the study of tree fine-root turnover with minirhizotrons. Plant Root 1:34-45.

Schoettle, A.W., and T.J. Fahey. 1994. Foliage and fine root longevity of pines, p. 136-153, *In* H. L. Gholz, et al., eds. Environmental constraints on the structure and productivity of pine forest ecosystems: a comparative analysis. Vol. 43. Ecological Bulletins, Copenhagen.

Silver, W., and R. Miya. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129:407-419.

Smith, R.L., and T.M. Smith. 2003. Elements of Ecology. 5th ed. Benjamin Cummings, San Fransisco, CA, USA.

Smucker, A.J.M. 1993. Soil environmental modifications of root dynamics and measurement. Ann. Rev. Phytopathol. 31:191-218.

Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17:577-587.

Strong, W.L., and G.H. La Roi. 1983a. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res. 13:577-588.

Strong, W.L., and G.H. La Roi. 1983b. Root-system morphology of common boreal trees in Alberta, Canada. Can. J. For. Res. 13:1164-1173.

Tennant, D. 1975. A test of a modified line intersect method of estimating root length. J. Ecol. 63:995.

Tierney, G.L., and T.J. Fahey. 2001. Evaluating minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest. Plant Soil 229:167-176.

Tingey, D.T., D.L. Phillips, and M.G. Johnson. 2000. Elevated CO_2 and conifer roots: effects on growth, life span and turnover. New Phytol. 147:87-103.

Vogt, K.A., and H. Persson. 1991. Measuring growth and development of roots, p. 477-501, *In* J. P. Lassoie and T. M. Hinckley, eds. Techniques and approaches in forest tree ecophysiology. CRC Press, Boca Raton.

Vogt, K.A., D.J. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 200:71-89.

Vogt, K.A., D.J. Vogt, P.A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159-219.

Volkmar, K.M. 1993. A comparison of minirhizotron techniques for estimating root length density in soils of different bulk densities. Plant Soil 157:239-245.

Wells, C.E., and D.M. Eissenstat. 2001. Marked differences in survivorship among apple roots of different diameters. Ecology 82:882-892.

Wells, C.E., and D.M. Eissenstat. 2003. Beyond the roots of young seedlings: the influence of age and order on fine root physiology. J. Plant Growth Regul. 21:324-334.

Wells, C.E., D.M. Glenn, and D.M. Eissenstat. 2002. Changes in the risk of fine-root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). Am. J. Bot. 89:79-87.

West, J.B., J.F. Espeleta, and L.A. Donovan. 2004. Fine root production and turnover across a complex edaphic gradient of a *Pinus palustris-Aristida stric*ta savanna ecosystem. For. Ecol. Manag. 189:397-406.

Zobel, R. 2003. Fine roots - discarding flawed assumptions. New Phytol. 160:276-279.

Zutter, B.R. 1999. Root length and biomass in mixtures of broomsedge with loblolly pine or sweetgum. Can. J. For. Res. 29:926.

3 FINE ROOT BIOMASS AND NET PRIMARY PRODUCTION IN THE BOREAL FOREST OF SASKATCHEWAN

3.1 Introduction

As anthropogenic carbon dioxide (CO_2) emissions continue to increase, global climate change is becoming a greater focus of the research community. In order to gain a better understanding of the various sinks and sources of CO_2, complex models are used to estimate global carbon (C) stocks. The two greatest C stocks in most models are the oceans and terrestrial forests, including tropical, temperate, and boreal forests (Falkowski et al., 2000; Malhi et al., 1999; Schindler, 1999). Globally, the Boreal Forest occupies 1.2 billion ha (Moore, 1996) and contain approximately 89.7 Mg C ha^{-1} in the vegetation with a further 208 Mg C ha^{-1} in the soils (Lal et al., 1997). Approximately 69 – 95% of the belowground C component is located in soil organic matter (SOM) with the remainder located in root biomass (Dixon et al., 1994; Malhi et al., 1999). The Boreal Forests contains on average 10.8 Mg C ha^{-1} in living roots, accounting for 2.6% of total belowground C stocks across the world (Gower et al., 1997; Malhi et al., 1999; Steele et al., 1997).

Fine roots (FR) are an inherently important component of ecosystem C studies. Traditionally, FR have been defined as roots with an arbitrary diameter of 1 – 10 mm or less with roots < 2 mm being the most common diameter (Johnson et al., 2001; Kalyn, 2005; Li et al., 2003; Pregitzer, 1998; Steele et al., 1997; Wells and Eissenstat, 2001; Wells et al., 2002). It has been estimated that FR can account for nearly one-third of global net primary productivity (Gill and Jackson, 2000). In coniferous forests, FR can be very important to belowground C cycling and a large potential C sink with 63 – 77% of total net primary production C being sequestered to the soil C pool (Fogel, 1983). Improving our knowledge of fine root dynamics is critical to gaining a better understanding of C storage and allocation in the world's forests (Cairns et al., 1997).

Estimating FR processes and parameters can be very difficult due to the high degree of variability associated with belowground dynamics. Destructive and non-destructive are the two main types of methodologies employed for studying FR. While destructive methods allow for analysis of the rooting system at one specific point in time, non-destructive methods such as minirhizotrons (MR) allow for repeated *in situ* root measurements over a long period of time (Hendrick and Pregitzer, 1996a; Johnson et al., 2001; Vogt et al., 1998).

The use of minirhizotrons (MR) in FR studies can be difficult both in theory and in practice. There are a number of methods available to convert the raw MR data into useable estimates of FR biomass and production. Unfortunately, there is no definitive answer as to which method is the best as they each have their own set of assumptions, strengths, and weaknesses. This study used the plane intersect method as suggested by Bernier and Robitaille (2004).

The objectives of this study were to 1) estimate the intra-annual variability of FR biomass and production values for four boreal forest sites in northern Saskatchewan across a four year time period using MR, 2), compare MR FR biomass values to those measured from sequential soil cores, and 3) compare FR C biomass and production to other ecosystem C pools.

3.2 Materials and methods

3.2.1 Site description

Four sites were selected from the Boreal Ecosystem Research and Monitoring Sites (BERMS) located in the boreal forest north of Prince Albert, Saskatchewan (Figure 3.1). The sites included a mature trembling aspen (*Populus tremuloides*) stand (OA), a mature black spruce (*Picea mariana*) stand (OBS), a mature jack pine (*Pinus banksiana*) stand (OJP), and a young jack pine stand (HJP94) harvested in 1994. A summary of various site characteristics can be found in Table 3.1.

The mature aspen site is a naturally regenerated stand dating back to a forest fire in 1919. The dominant tree species is trembling aspen with a beaked hazel (*Corylus cornuta*) understory. The OA site is located near the south edge of the Prince Albert National Park (UTM 420790.5, 5942899.9), northwest of Prince Albert at an elevation of 600 m. The dominant soils in the area are Orthic Gray Luvisols (Soil Classification Working Group, 1998) on glacial till parent material.

The OBS site is a 100-150 year old naturally regenerated stand. The dominant species is black spruce interspersed with tamarack (*Larix larcina*) and jack pine. The understory is comprised of primarily of mosses, Labrador tea (*Ledum groenlandieum*), and prickly rose (*Rosa acicularis*). The site is located northeast of Candle Lake (UTM 492843, 5981904) at an elevation of 628 m. Soils at the OBS site are classified as Gleyed Eluviated Eutric Brunisols (Soil Classification Working Group, 1998).

The OJP (UTM 520285, 5974904) and HJP (UTM 523285, 5969705) sites are located near the Narrow Hills Provincial Park, northeast of Prince Albert. The OJP site regenerated naturally after fire. The HJP site was harvested in 1994 and also regenerated

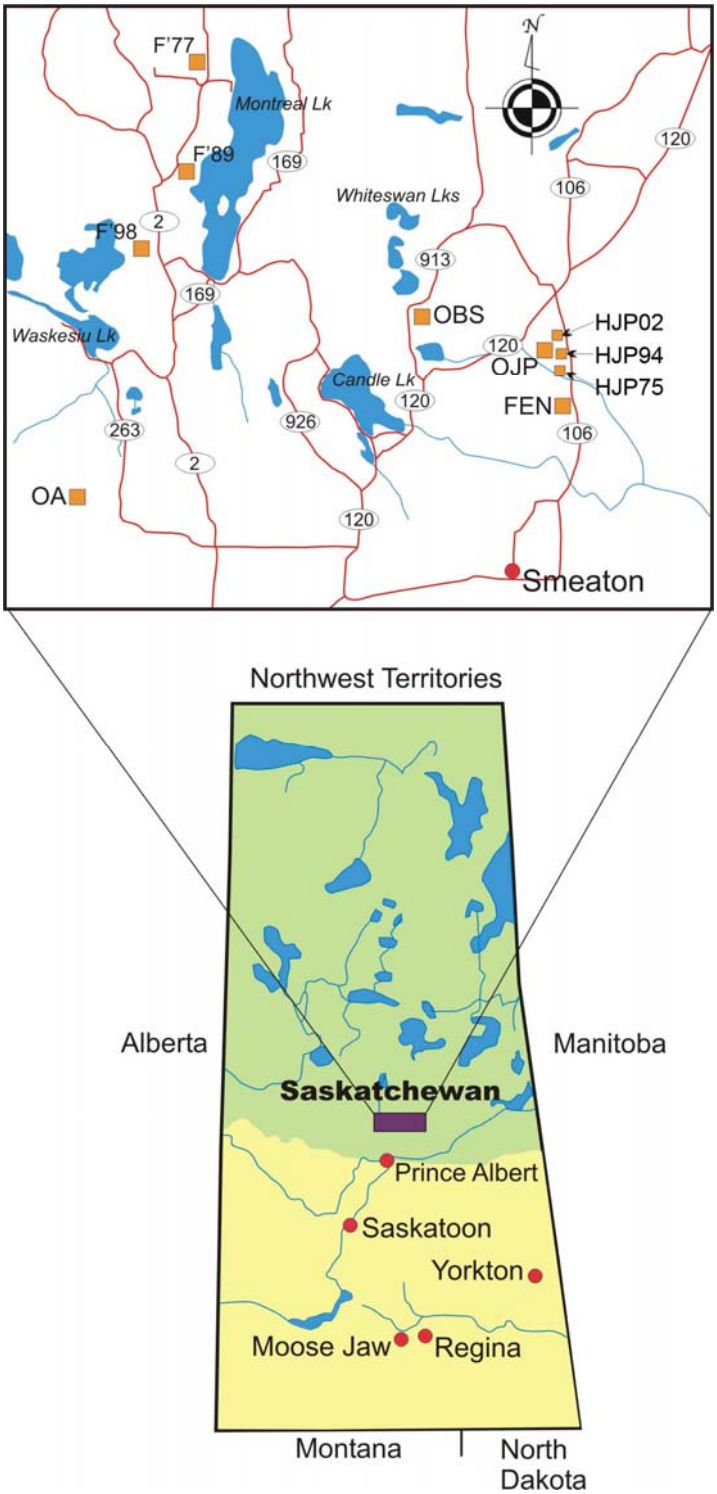

Figure 3.1: Site locator map of Saskatchewan showing the Boreal Ecosystem Research and Monitoring Sites (BERMS) study area and the locations of Old Aspen (OA), Old Black Spruce (OBS), Old Jack Pine (OJP), and Harvested Jack Pine '94 (HJP94) (image courtesy Fluxnet Canada, 2007)

Table 3.1: Selected stand characteristics for the black spruce (OBS), aspen, (OA), jack pine (OJP), and harvested jack pine (HJP) Boreal Ecosystem Research and Monitoring Sites (BERMS) in northern Saskatchewan (adapted from Kalyn and Van Rees, 2006).

		Stand Characteristics								
Site	Location†	Age	Trees	Average DBH ‡	Mean Tree Height	Basal Area	Soil Order	Soil Drainage Class	LFH Depth	Soil Texture
		years	No. ha^{-1}	cm	m	m^2 ha^{-1}			cm	
OBS	N:5,981,904 E:492,843	123	4330	7.1	7.2	35.6	Gleyed Eluviated Eutric Brunisol (Peaty phase ¶)	Imperfect to Poor	20-30	Sandy loam to loam till
OA	N:5,942,649 E:420,843	84	980	20.5	20.1	26.7	Orthic Gray Luvisol	Well to Moderately well	< 8	Loam to clay loam till
OJP	N:5,974,904 E:520,285	88	1320	12.9	12.7	13.3	Orthic Eutric Brunisol	Very well	< 5	Fine sand
HJP	N:5,969,705 E:523,285	11	4056	3.2	3.7	9.1	Orthic Eutric Brunisol	Very well	< 3	Fine sand

† UTM Zone 13.

‡ Tree diameter at breast height.

¶ Any mineral soil having a surface horizon of 15-60 cm of fibric organic material may be designated as a peaty phase (Soil Classification Working Group, 1998).

naturally. The dominant species at each of these two sites is jack pine. The understory at OJP and HJP consists primarily of reindeer lichen (*Cladonia spp*.) and kinnikinick (*Arctostaphylos uva-ursi*). There are also some small clumps of green alder (*Alnus crispa*) at the HJP site. The soils of the area are dominantly Orthic Eutric Brunisols (Soil Classification Working Group, 1998) on a fine sand parent material.

3.2.2 Fine root measurement using minirhizotrons

A total of twelve MR were installed during the summer of 2002 at each of the four study sites: OA, OBS, OJP, and HJP94. The MR were installed in three banks of four tubes along three transects to minimize spatial variation. The MR observation tubes are made of cellulose acetate butyrate (CAB) with an inside diameter of 50.8 mm. The bottom end of each tube is sealed with a machined plastic plug. A steel core extractor with a reverse bevel cutting tip is driven into the ground with a Pacepik Model 2550 (Williams and James Engineers, Ltd., Glouchester, GB) gas-powered hydraulic powerpack and jackhammer at an angle of 38˚ to the horizontal (Figure 3.2). The reverse-bevel tip compresses the soil core inside the steel extraction tube, which reduces the disturbance to the soil outside the tube and helps minimize the chances of an uneven soil-tube interface when the MR observation tube is installed. The MR observation tubes are installed in the core holes to a vertical depth of approximately 75 cm. Due to the high clay content and stoniness of the soil at the OA site, the tubes were installed as deep as possible ranging from 38 – 51 cm vertically. After the tubes had been installed in the ground they were secured by driving two 90 cm long pieces of rebar into the ground on each side of the tube and attaching the tubes to the rebar with two industrial cable-ties. The aboveground portions of the tubes were painted black and then white to minimize light entering the tube and heating of the tube from solar radiation.

Minirhizotron root images were collected at the end of each month from May through September for 2003 to 2006 from three of the four tubes in each bank (images from the fourth tubes were collected for the image orientation study in Chapter 5 prior to being excavated). Minirhizotron images from the 2003 and 2004 field seasons were collected and analyzed by Amanda Kalyn as part of her Master's thesis. Root images were taken using a modified video camera on an indexed handle (Bartz Technology Co., Santa Barbara, CA, USA). The increments on the indexed handle are spaced at 1.2 cm. The root images were saved to a Sony notebook computer using Bartz Technology Company's I-CAP software.

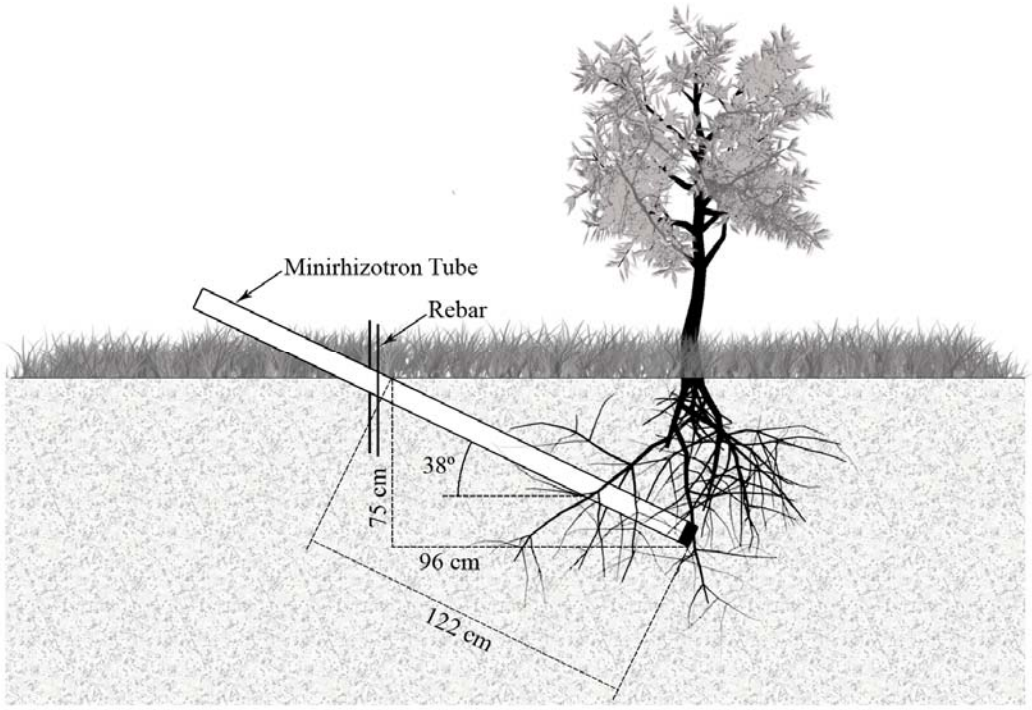

Figure 3.2: Schematic diagram showing an installed cellulose acetate butyrate (CAB) minirhizotron tube. Inner tube diameter is 5.08 cm.

After the root images were collected in the field, they were then transferred to a lab computer for analysis. The analysis of the images consists of tracing the length and width (diameter) of visible roots in each image using the RooTracker root analysis software (Version 2.0.3b1, Duke University, NC, USA). After root tracing was completed, RooTracker data was exported to Microsoft Excel where the data of interest were extracted and stored in another file for further analysis using the plane intersect method.

The plane intersect method proposed by Bernier and Robitaille (2004) expands on Van Wagner's (1968) line intersect method for estimating forest fuel loads. The plane intersect method (PIM) uses the diameter and date of FR appearance to estimate biomass and productivity (whereas productivity is the difference in biomass between two months) as they were deemed the most robust variables that can be obtained from the MR FR measurements. The basis of the PIM is that if a given volume of soil was sliced into an infinite number of slices, the area of the roots intersecting an individual slice (cross sectional root area) is divided by the area of the slice. Then, the sum of the root area for all of the slices gives an estimate of the total volume of root per unit volume of soil. For more details on the plane intersect method and its theory, please refer to Bernier and Robitaille (2004). For the purposes of this project, the PIM was implemented in the form of a SAS (Version 9.1, SAS Institute Inc, Cary, NC, USA) script (Appendix A) that utilizes two input files. The first file consists of data from the RooTracker output such as tube number, frame number, root number, sample date (in Julian day), and root diameter. The second input file consists of physical information about the tubes including tube number, angle of the tube from horizontal, ground slope, stone fraction of the soil (OA – 0.10, OBS – 0.01, OJP – 0.001, and HJP – 0.001 (Kalyn, 2005)), and an average specific root mass (OA – 0.442, OBS – 0.469, OJP – 0.613, and HJP – 0.573 (Kalyn, 2005)). Fine root biomass and productivity output values from the PIM were then statistically analyzed. Values for FR biomass and production were converted to measurements of FR biomass C and C production. The conversion to C values was done using site-specific FR C contents measured by Kalyn (2005) (40%, 38%, 46%, and 48% for HJP94, OJP, OA, and OBS, respectively).

3.2.3 Soil coring methodology and laboratory analysis

Fine root biomass was sampled in August of 2005 using the soil coring method as described by Kalyn (2005). A total of 36 cores were collected with a bucket auger (10 cm dia.) near each of the nine primary MR tubes at OA, OBS, OJP, and HJP94 in depth increments of 0 – 5, 5 – 15, 15 – 25, and 25 – 35 cm. The soil cores were stored in

coolers in the field. Once back in the lab, the soil cores were frozen at -4ºC until they were analyzed.

Prior to analysis, the soil cores were thawed at room temperature for several days. The soil cores were hand washed in large basins in sacks of gathered window screen. Roots were picked from the debris on the screens and washed again in clean water. Fine root diameters were visually assessed using a guide card. The roots were separated into two diameter size classes of ≤ 2 mm and > 2 mm. While roots > 2 mm were counted and recorded, they were not used directly in this study. A 2 mm diameter class was used to directly compare SSC biomass values with those calculated using the MR method. It should be noted that this study sought to determine total FR biomass, not live root biomass. As such, there was no effort made to separate live from dead roots. This decision was made so as to sample the entire root population found within a core similar to the root populations sampled using the MR technique where roots are measured until they have disappeared. After washing, all roots were oven dried at 60ºC for approximately 48 hours. Root dry weights were then measured and recorded.

3.2.4 Soil moisture and temperature

Soil volumetric water content (VWC) and soil temperatures were collected at HJP94, OJP, OA, and OBS. Volumetric water content was recorded every 30 minutes from one or more pits using Campbell Scientific CS615 soil moisture probes (Campbell Scientific, Edmonton, AB, Canada) at depths of 0 – 15, 15 – 30, 30 – 45, and 45 – 60 cm at HJP94 and OJP; 2.5, 7.5, 15 – 30, and 30 – 60 cm at OA; and 2.5, 7.5, 22.5, and 45 cm at OBS. Soil temperature was recorded in 30 minute intervals from one or more soil pits at each site using Campbell Scientific 105T copper-constantan thermocouple probes (Campbell Scientific, Edmonton, AB, Canada) at depths of 2, 5, 10, 20, and 50 cm. For the purposes of this study, soil VWC was averaged over a depth interval of 0 – 60 cm, while soil temperature was averaged over an interval of 0 – 50 cm. Soil moisture and temperature data were collected and post-processed by the BERMS project. Mean daily soil VWC and soil temperature can be seen in Appendix C.

3.2.5 Total ecosystem carbon production and biomass

Adapted from Kalyn (2005) and Theede (2007), estimates of C production and biomass for various ecosystem components were collected from several different studies. Carbon biomass distribution values for the HJP94 and OJP sites were taken from Howard et al. (2004), while data for the OA and OBS sites were from Gower et al. (1997) and Steele et al. (1997). Biomass C estimates for the FR component were from MR data

collected in this study from 2003 to 2006. Ecosystem C production estimates for HJP were from Howard et al. (2004), OJP and OA estimates were adapted from Theede (2007), and data for OBS were gathered from Gower et al. (1997) and Steele et al. (1997). All FR C production data was from this study and was collected from 2003 to 2006.

3.2.6 Statistical analysis

The plot layout of this study was a nested design with each bank of MR tubes considered an independent nest (Hendrick and Pregitzer, 1992b). Statistical analyses in this study were completed using a combination of SAS and SPSS (SPSS for Windows, Release 14.0.0, SPSS Inc, Chicago, IL, USA) statistical software packages. Initial application of the PIM to the raw MR data was done using SAS (Bernier and Robitaille, 2004). All FR biomass and production data were square root transformed to fit a normal distribution and were analyzed using repeated measures ANOVA in SPSS. Differences in FR biomass estimates between soil cores and MR were tested with paired-means *t*-tests in SPSS (Field, 2005). Multiple linear regressions using a backward stepwise method in SPSS were used to estimate the influence of soil moisture and soil temperature on FR biomass and production over a four year period at each research site. The backward method for regressions includes all parameters in the first iteration. In following iterations, the program tests each factor against a removal criterion and will remove the factor that has the least influence on the outcome and run the regression again. Pearson correlation values were also calculated for soil temperature and moisture against FR biomass and production. All statistical analyses were done using a 90% confidence interval ($\alpha = 0.1$) to account for the variability in a natural ecosystem, while not being so rigid as to miss possible significant effects (Pennock, 2004, Peterson, 1990).

3.3 Results

3.3.1 Minirhizotron estimates of fine root biomass and production

Fine root biomass was estimated for MR data from HJP94, OJP, OA, and OBS from June to October in 2003, 2004, 2005, and 2006 using the plane intersect method. The total number of FR analyzed generally increased from 2003 to 2006 (approximately 3, 7, 10, and 24 times greater at OBS, HJP94, OJP, and OA respectively), with OBS having the greatest number of roots (Figure 3.3). Average monthly FR biomass also increased from 2003 to 2006; however, there were also increasing and decreasing annual cycles in all years except 2005 at all four sites (Figure 3.4). Monthly FR biomass to a 40

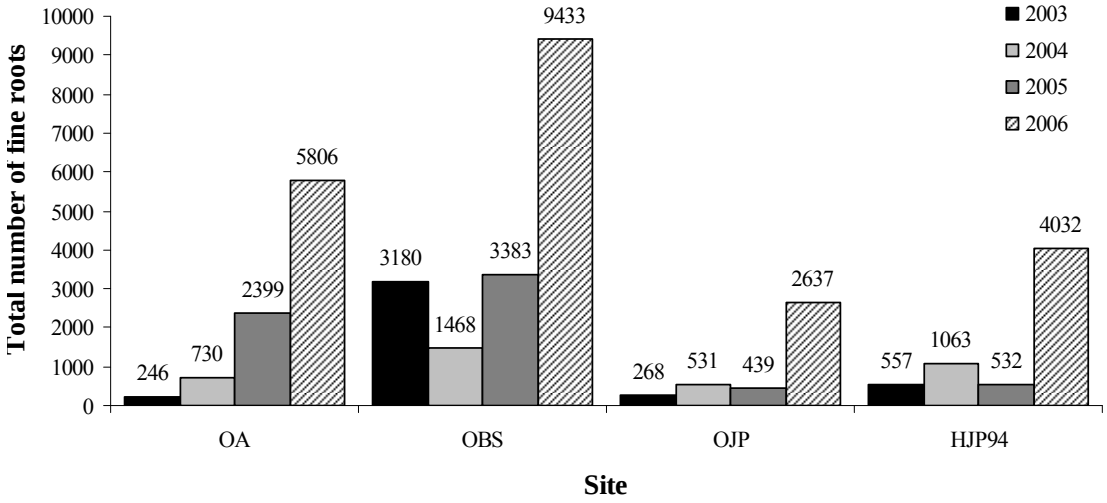

Figure 3.3: Total number of fine roots analyzed to a vertical depth of 40 cm using the minirhizotron techniques for four boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006.

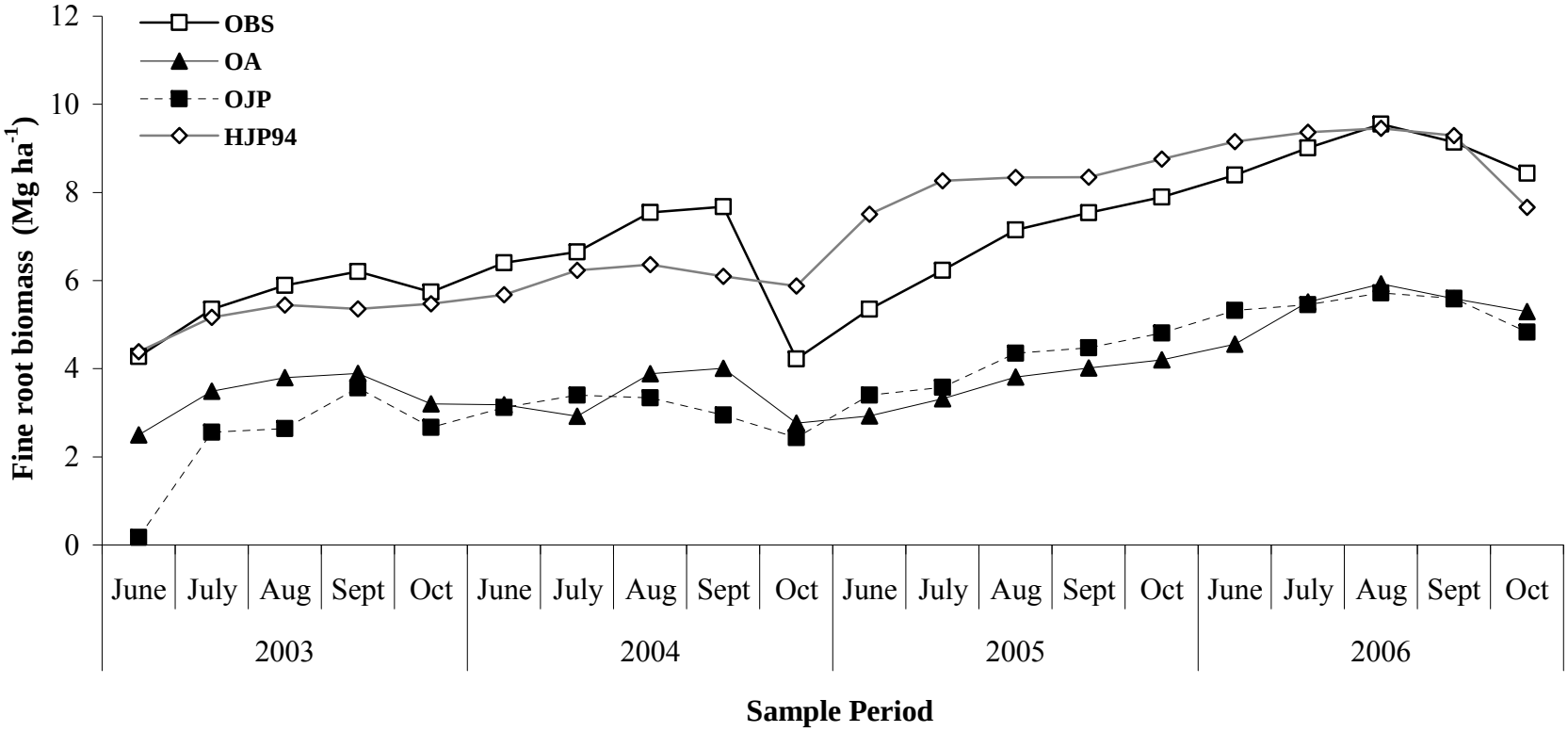

Figure 3.4: Fine root biomass estimates from minirhizotron data using the plane intersect method at Old Aspen, Old Black Spruce, Old Jack Pine, and Harvested Jack Pine 94 for 2003 to 2006 growing seasons.

cm depth ranged from 0.019 ± 0.171 Mg ha^{-1} at OJP in June of 2003 to 8.82 ± 0.827 Mg ha^{-1} in August of 2006 at OBS (Table 3.2). A large drop in FR biomass at OBS in 2004 for the September/October interval was noted. The highest monthly FR biomass for each site occurred in July/August of 2006. During the four years of measurements, FR biomass values were consistently higher at OBS and HJP94 and nearly double those of OA and OJP (Figure 3.4). The only years that did not have significant differences between months were at HJP in 2004 and OJP in 2005, respectively (Appendix B (Table B.1)). Mean annual FR biomass showed no significant differences between any of the four years at HJP94, while significant differences were found at the other three sites (Table 3.3). Values for mean annual biomass generally increased from 2003 to 2006 at all sites and were highest for HJP94 and OBS (~8 Mg ha^{-1}).

Fine root production was estimated from MR data on a monthly basis from 2003 to 2006 inclusively for the months of June through October with production being the difference in biomass between two months. Repeated measures ANOVA showed that there was a significant effect of months between years on FR production at HJP94, OJP, OA, and OBS (p = 0.016, 0.010, 0.000, and 0.001, respectively) while differences between years showed a significant effect on FR production at OA (p = 0.003) (Appendix B (Table B.2). Repeated measures analysis results for monthly FR production within years can be found in Appendix B (Table B.3). Seasonal variation in FR production was generally greatest in the early months of summer and then tapered off into fall (Fig. 3.5). Fine root production was highest in June of 2003 at HJP94 and OBS and in July at OJP and OA with values of 2.09, 1.64, 1.00, and 1.56 Mg ha^{-1} mo^{-1}, respectively (Table 3.4). In October of 2003, FR production at OJP fell below zero (-0.552 Mg ha^{-1} mo^{-1}) as a result of more biomass lost than created between September and October. Mean annual FR net primary productivity (NPP) estimates from MR data ranged from 1.07 Mg ha^{-1} yr^{-1} at HJP94 in 2006 to 4.01 Mg ha^{-1} yr^{-1} at OA in 2003 (Table 3.5). No significant differences were found in mean annual FR NPP estimates at any of the four sites from 2003 to 2006 (Table 3.5).

3.3.2 Fine root biomass, productivity, and soil environmental factors.

The four years examined in this study covered a broad range of environmental conditions from severe, long-term drought in 2002 and 2003 to cool and extremely wet conditions in 2005 and 2006 (Appendix C). Soil volumetric water content and soil temperature were tested as predictors of FR biomass and production. Soil temperature was found to have a significant positive effect on FR biomass at OJP, OA, and OBS and

Table 3.2: Mean monthly fine root biomass based on minirhizotron data to a vertical depth of 40 cm at four boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan for 2003 to 2006. Values in parentheses represent 1 SD (n = 9).

		Mean Fine Root Biomass			
Site	Month	2003	2004	2005	2006
		---------- Mg ha^{-1} ----------			
HJP94	June	3.25 (1.27) b†	4.75 (1.04) a	6.45 (1.19) a	8.33 (0.928) b
	July	3.93 (1.94) ab	5.37 (0.974) a	7.29 (1.10) a	8.54 (0.931) a
	August	4.33 (1.26) a	5.57 (0.889) a	7.37 (1.09) a	8.62 (0.940) a
	September	2.24 (1.26) ab	5.37 (0.819) a	7.39 (1.08) a	8.38 (1.03) ab
	October	4.46 (1.14) a	5.13 (0.836) a	7.96 (0.899) a	6.92 (0.835) b
OJP	June	0.0190 (0.171) c	2.84 (0.315) a	3.13 (0.299) c	4.88 (0.499) bc
	July	2.45 (0.120) b	3.17 (0.260) a	3.33 (0.279) bc	5.00 (0.508) b
	August	2.54 (0.120) b	3.16 (0.207) a	3.94 (0.471) b	5.24 (0.542) a
	September	3.44 (0.141) a	2.78 (0.192) a	4.07 (0.460) b	5.07 (0.593) ab
	October	2.51 (0.178) b	2.30 (0.151) a	4.35 (0.521) a	4.29 (0.613) c
OA	June	2.25 (0.277) c	2.71 (0.526) c	2.53 (0.440) e	3.92 (0.717) c
	July	3.32 (0.196) ab	2.41 (0.576) c	2.82 (0.558) d	4.88 (0.715) b
	August	3.43 (0.417) a	3.27 (0.689) b	3.25 (0.627) c	5.32 (0.682) a
	September	3.43 (0.518) a	3.42 (0.660) a	3.45 (0.633) b	4.98 (0.685) ab
	October	2.76 (0.502) bc	2.38 (0.428) c	3.60 (0.673) a	4.71 (0.656) b
OBS	June	2.96 (1.49) d	5.37 (1.16) b	4.56 (0.891) e	7.67 (0.815) d
	July	4.22 (1.27) c	5.55 (1.23) b	5.37 (0.972) d	8.31 (0.789) bc
	August	4.83 (1.19) b	6.53 (1.14) a	6.26 (1.00) c	8.82 (0.827) a
	September	5.17 (1.16) a	6.58 (1.24) a	6.64 (1.00) b	8.46 (0.762) b
	October	4.77 (1.10) abc	7.09 (0.903) c	7.09 (0.903) a	7.67 (0.857) cd

† For each site, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using repeated measures ANOVA.

Table 3.3: Mean annual fine root biomass to a vertical depth of 40 cm for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006. Values in parentheses represent 1 SD (N=45).

	Mean Annual Fine Root Biomass			
Year	HJP94	OJP	OA	OBS
	---------- Mg ha^{-1} ----------			
2003	4.04 (6.25) a†	1.82 (0.573) c	3.03 (1.77) ab	4.36 (6.10) ab
2004	5.24 (4.41) a	2.86 (1.00) b	2.82 (2.76) b	5.48 (5.11) ab
2005	7.29 (5.29) a	3.76 (1.99) ab	3.13 (2.89) b	5.95 (4.75) b
2006	8.12 (4.62) a	4.88 (2.72) a	4.75 (3.39) a	8.18 (4.00) a

† Means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using repeated measures ANOVA

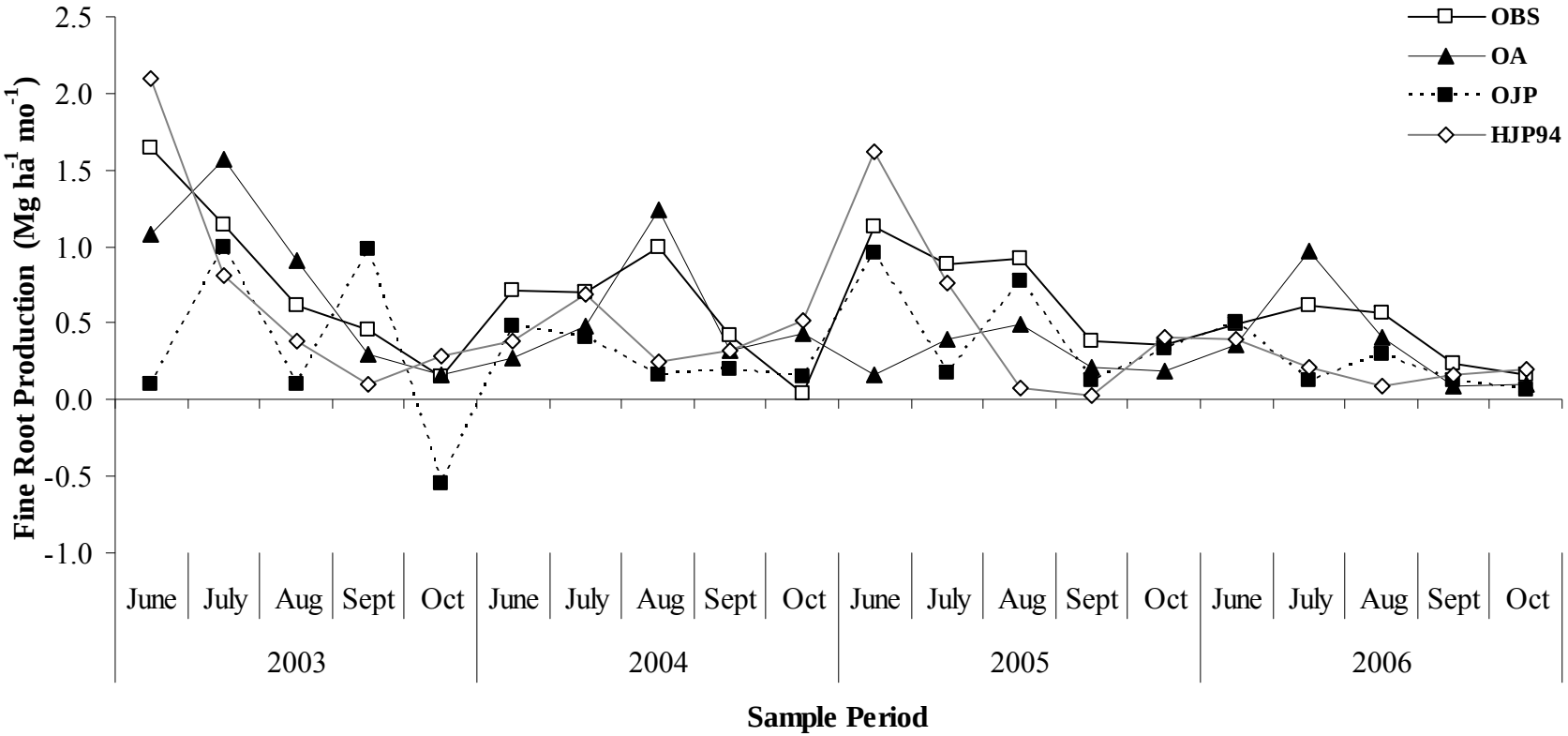

Figure 3.5: Fine root production estimates from minirhizotron data to a vertical depth of 40 cm using the plane intersect method at Old Aspen (OA), Old Black Spruce (OBS), Old Jack Pine (OJP), and Harvested Jack Pine 94 (HJP94) for 2003 to 2006 growing seasons.

Table 3.4: Mean monthly fine root production based on minirhizotron data from four boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan for 2003 to 2006. Values in parentheses represent 1 SD (n = 9).

		Mean Fine Root Production			
Site	Month	2003	2004	2005	2006
		---------- Mg ha^{-1} mo^{-1} ----------			
HJP94	June	2.09 (3.83) a†	0.388 (0.324) a	1.62 (3.01) a	0.395 (4.12) a
	July	0.806 (0.979) a	0.688 (0.916) a	0.765 (0.824 a)	0.217 (0.172) a
	August	0.388 (0.698) a	0.246 (0.583) a	0.0753 (0.0917) a	0.0922 (0.112) a
	September	0.0973 (0.124) a	0.325 (0.295) a	0.022 (0.051) a	0.164 (0.251) a
	October	0.289 (0.483) a	0.517 (0.504) a	0.411 (0.483) a	0.202 (0.182) a
OJP	June	0.101 (0.303) ab	0.481 (0.933) a	0.961 (1.23) a	0.510 (0.964) a
	July	1.00 (1.19) a	0.408 (0.274) a	0.178 (0.197) a	0.132 (0.126) a
	August	0.0975 (0.139) a	0.158 (0.119) a	0.779 (1.23) a	0.293 (0.257) a
	September	0.982 (0.827) a	0.195 (0.382) a	0.120 (0.180) a	0.131 (0.126) a
	October	-0.552 (0.659) b	0.155 (0.282) a	0.335 (0.400) a	0.0589 (0.0518) a
OA	June	1.08 (0.654) a	0.269 (0.384) a	0.161 (0.134) a	0.357 (0.545) ab
	July	1.56 (0.528) a	0.478 (0.694) a	0.391 (0.573) a	0.964 (1.10) ab
	August	0.913 (1.21) ab	1.24 (1.09) a	0.492 (0.653) a	0.413 (0.247) b
	September	0.302 (0.525) b	0.316 (0.240 a)	0.206 (0.174) a	0.0871 (0.0648) a
	October	0.157 (0.230) b	0.433 (0.461) a	0.184 (0.325) a	0.105 (0.130) ab
OBS	June	1.64 (2.62) ab	0.708 (0.780) ab	1.13 (1.70) a	0.496 (0.429) ab
	July	1.14 (0.823) a	0.697 (0.469) a	0.880 (0.667) a	0.620 (0.387) a
	August	0.612 (0.361) a	0.996 (0.824) a	0.916 (0.577) a	0.565 (0.603) ab
	September	0.453 (0.254) ab	0.421 (0.286) a	0.388 (0.252) a	0.241 (0.156) b
	October	0.155 (0.185) b	0.0358 (0.0775) b	0.360 (0.299) a	0.161 (0.0526) b

† For each site, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using repeated measures ANOVA.

Table 3.5: Mean annual fine root net primary productivity to a vertical depth of 40 cm for four BERMS boreal forest sites, including harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006. Values in parentheses represent 1 SD (N=45).

	Fine Root Net Primary Production			
Site	HJP94	OJP	OA	OBS
	---------- Mg ha^{-1} yr^{-1} ----------			
2003	3.67 (4.64) a†	1.63 (1.65) a	4.01 (2.55) a	4.00 (2.96) a
2004	2.16 (1.60) a	1.40 (1.14) a	2.73 (2.18) b	2.86 (1.64) a
2005	2.90 (3.31) a	2.37 (2.71) a	1.43 (1.51) c	3.67 (2.66) a
2006	1.07 (0.714) a	1.12 (1.36) a	1.93 (1.32) abc	2.08 (0.743) a

† Means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using repeated measures ANOVA

significant negative effect on FR production at OBS (Table 3.6). Soil moisture and soil temperature were found to have positive and negative significant effects, respectively, on FR production at HJP94. Soil volumetric water content and temperature both affected FR biomass and production, although neither was dominant in the regression equations across the sites (Table 3.7). Multiple linear regression models using soil volumetric water content and soil temperature were found to be most successful for FR biomass at OA and OBS ($p = 0.000$, $R^2 = 0.601$ and $p = 0.007$, $R^2 = 0.438$, respectively) and for FR production at HJP94 ($p = 0.010$, $R^2 = 0.421$).

3.3.3 Comparison of fine root biomass from soil cores and minirhizotrons

Fine root biomass collected from soil cores in August 2005 was compared with estimates from the MR method from images collected at the same time (Figure 3.6). Biomass estimates at OJP, OA, and OBS were similar between the SSC and MR methods; however, FR biomass estimates for the MR method were significantly greater (3.74 times) than the SSC method at HJP94 (Table B.4). The effect size (r) for the difference in FR biomass at HJP94 between the two methods was found to be 0.816. Values over 0.5 are considered to be important effects (Field, 2005) (Table B.4).

3.3.4 Distribution of ecosystem biomass carbon and carbon production

Total ecosystem C was estimated to be 47.5, 78.1, 163.1, and 450.5 Mg ha^{-1} for HJP94, OJP, OA, and OBS, respectively (Table 3.8). The belowground components contained the majority of ecosystem C at HJP94 (84%) and OBS (88%), while the aboveground components were dominant at OJP (53%) and OA (63%). The majority of the belowground C was found in the forest floor and the mineral soil at all sites. The contribution of FR to total ecosystem C ranged from 0.7 Mg ha^{-1} (1%) at OJP to 1.2 Mg ha^{-1} (< 1%) at OBS, while the coarse root component ranged from 0.3 Mg ha^{-1} (< 1%) at HJP94 to 6.0 Mg ha^{-1} (8%) at OJP. The three compartments contributing the most to ecosystem C at each site were stems (3 to 51%), forest floor (11 to 23 %), and mineral soil (22 to 87%).

Total ecosystem C production ranged from 2.1 Mg ha^{-1} yr^{-1} at HJP94 to 4.8 Mg ha^{-1} yr^{-1} at OBS (Table 3.9). Total belowground C production represented the greatest portion at HJP94 (57%) and OBS (65%) while only accounting for 36% at OJP and 31% at OA. Fine root C production was estimated at 1.0, 0.6, 1.2, and 1.5 Mg ha^{-1} yr^{-1} accounting for 47, 27, 25, and 54% of total ecosystem C production at HJP94, OJP, OA, and OBS, respectively.

Table 3.6: Pearson correlations for fine root biomass and production from minirhizotrons as related to soil moisture [volumetric water content (m^3/m^3)] and soil temperature (ºC) to a vertical depth of 40 cm for four boreal forest sites in northern Saskatchewan, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands for 2003 to 2006 combined (n=20 per site).

Site	Soil Parameter	Pearson Correlation Value	Sig. (1-tailed)
		Fine Root Biomass	
HJP94	Temperature	0.054	0.410
	Moisture	0.108	0.325
OJP	Temperature	0.414	0.035*
	Moisture	-0.235	0.159
OA	Temperature	0.647	0.001*
	Moisture	0.420	0.482
OBS	Temperature	0.548	0.006*
	Moisture	0.283	0.114
		Fine Root Production	
HJP94	Temperature	-0.601	0.003*
	Moisture	0.614	0.000*
OJP	Temperature	-0.200	0.199
	Moisture	-0.019	0.469
OA	Temperature	-0.077	0.373
	Moisture	-0.239	0.155
OBS	Temperature	-0.385	0.047*
	Moisture	0.008	0.487

* denotes significance at $\alpha = 0.1$

Table 3.7: Multiple linear regressions of fine root biomass and production from minirhizotrons as related to soil moisture (m) [volumetric water content (m^3/m^3)] and soil temperature (t) (ºC) to a vertical depth of 40 cm for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan for 2003 to 2006 combined (n=20 per site). Data were transformed to fit a normal distribution.

Site	Iteration	Multiple Linear Regression Equation	*Moisture p-value*	*Temperature p-value*	*Model p-value*	Model R^2
		Fine Root Biomass				
HJP94	1	Sqrt Biomass = 1.03 + 10.7 (m) + 0.034 (t)	0.350	0.394	0.622	0.054
	2	Sqrt Biomass = 2.13 + 3.36 (m)	0.650		0.650	0.012
OJP	1	Sqrt Biomass = 0.812 + 3.71 (m) + 0.064 (t)	0.631	0.121	0.179	0.183
	2	Sqrt Biomass = 1.27 + 0.0500 (t)		0.070*	0.070*	0.171
OA	1	Sqrt Biomass = 0.911 + 1.02 (m) + 0.056 (t)	0.013*	0.001*	0.000*	0.601
OBS	1	Sqrt Biomass = 1.43 + 1.99 (m) + 0.060 (t)	0.057*	0.004*	0.007*	0.438
		Fine Root Production				
HJP94	1	ln Prod = 2.77 + 31.1 (m) – 0.091 (t)	0.200	0.272	0.010*	0.421
	2	ln Prod = -5.78 + 51.1 (m)	0.004*		0.004*	0.377
OJP	1	ln Prod = 1.04 -15.7 (m) – 0.105 (t)	0.294	0.183	0.400	0.102
	2	ln Prod = -0.886 – 0.440 (t)		0.398	0.398	0.040
OA	1	ln Prod = -0.030 – 2.00 (m) – 0.024 (t)	0.322	0.738	0.573	0.063
	2	ln Prod = -0.267 – 1.99 (m)	0.311		0.311	0.057
OBS	1	ln Prod = 0.243 – 0.777 (m) – 0.109 (t)	0.819	0.100	0.249	0.151
	2	ln Prod = -0.220 – 0.107 (t)		0.094	0.094*	0.148

* denotes significance at $\alpha = 0.1$

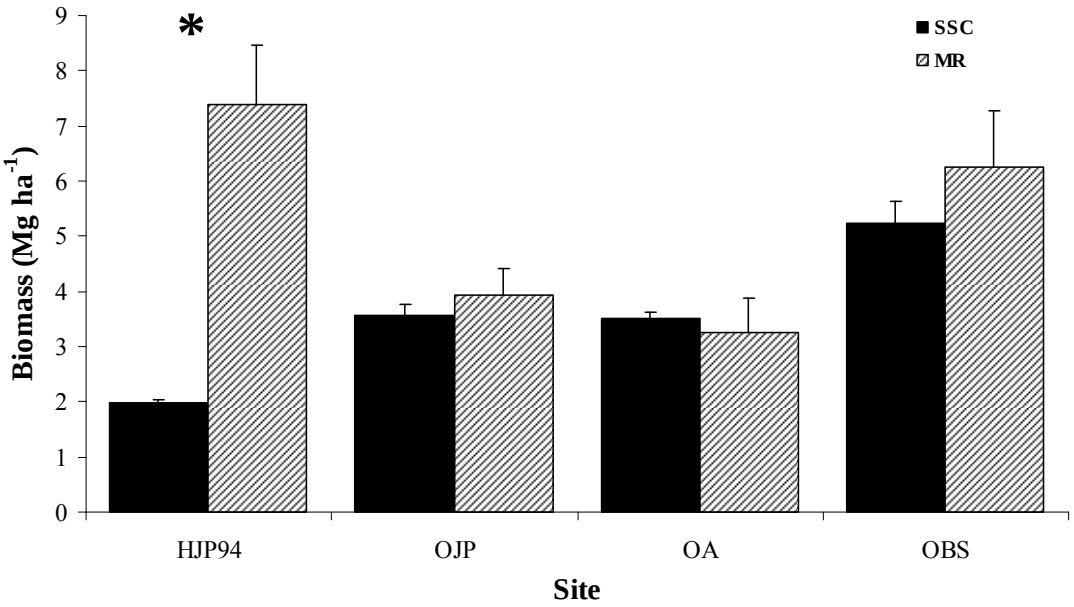

Figure 3.6: Comparison of fine root biomass to a 35 cm vertical depth determined using sequential soil coring and the minirhizotron technique for August 2005.
* denotes significant difference within a site using paired-means *t*-tests, $\alpha = 0.1$. Vertical bars denote 1 SD, n=9.

Table 3.8: Ecosystem carbon biomass distribution by component for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan. Values in parentheses are the contribution of each component to the total ecosystem C biomass (%).

Ecosystem Component	HJP94†	OJP†	OA‡	OBS‡
	---------- Mg C ha^{-1} ----------			
		Living vegetation		
Stem	1.4 (3)	26.6 (34)	82.7 (51)	36.3 (8)
Branch	0.6 (1)	4.2 (5)	8.9 (5)	6.7 (1)
Foliage	0.8 (2)	1.1 (1)	0.9 (1)	5.1 (1)
Understory	0.8 (2)	0.1 (<1)	0.7 (<1)	0.5 (<1)
Coarse roots	0.3 (<1)	6.0 (8)	4.2 (3) §	3.5 (1)
Fine roots ¶	1.0 (2)	0.7 (1)	0.8 (<1)	1.2 (<1)
		Detritus/mineral soil		
Coarse woody debris	3.8 (8)	3.2 (4)	0 (0)	0.6 (<1)
Standing dead	0.0 (0)	6.7 (9)	9.6 (6)	6.2 (1)
Forest floor	10.9 (23)	8.6 (11)	19.4 (12)	-#
Mineral soil	27.9 (59)	20.9 (27)	35.9 (22)	390.4 (87)
Total aboveground	7.4 (16)	41.9 (53)	102.8 (63)	55.4 (12)
Total belowground	40.1 (84)	36.2 (47)	60.3 (37)	395.1 (88)
Total ecosystem carbon	47.5 (100)	78.1 (100)	163.1 (100)	450.5 (100)

† Values for HJP and OJP were taken from Howard et al. (2004) (1999 10 yr and 79 yr data).
‡ Values for OA and OBS were taken from Gower et al. (1997) and Steele et al. (1997).
§ Coarse root estimates for OA and OBS were taken from Steele et al. (1997)
¶ Fine root values were derived from minirhizotron biomass estimates from 2003 to 2006 in this study.
# Organic layer is included with the mineral soil component.

Table 3.9: Distribution of ecosystem carbon net primary production (NPP) by component for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan. Values in parentheses are the contribution of each component to the total ecosystem C production (%).

Ecosystem Component	HJP94†	OJP ‡	OA‡	OBS §
	----------Mg C ha^{-1} yr^{-1}----------			
Living vegetation				
Stem	0.4 (19)	0.7 (32)	1.3 (27)	0.8 (29) ¶
Branch	0.2 (10)	0.3 (14)	0.5 (10.5)	
Foliage	0.2 (10)	0.0 (0)		0.1 (3)
Understory	0.1 (4)	0.0 (0)	0.5 (10.5)	0.1 (3)
Coarse roots	0.2 (10)	0.2 (9)	0.3 (6)	0.3 (11) #
Fine roots ††	1.0 (47)	0.6 (27)	1.2 (25)	1.5 (54)
Detritus (foliar litter)		0.4 (18)	1.0 (21)	
Other detritus		0.0 (0)		
Total aboveground	0.9 (43)	1.4 (64)	3.3 (69)	1.0 (35)
Total belowground	1.2 (57)	0.8 (36)	1.5 (31)	1.8 (65)
Total ecosystem	2.1 (100)	2.2 (100)	4.8 (100)	2.8 (100)

† Values for HJP were taken from Howard et al. (2004) (1999 10 yr data).
‡ Values for OJP and OA were adapted from Theede (2007)
§ Values for OBS were taken from Gower et al. (1997) and Steele et al. (1997).
¶ Stem and branch C estimates were combined for OBS (Gower et al., 1997).
# Coarse root estimates for OBS were taken from Steele et al. (1997)
†† Fine root values were derived from minirhizotron production estimates from 2003 to 2006 in this study.

3.4 Discussion

3.4.1 Fine root biomass and production estimates from minirhizotron data

This study employed the use of MR and the PIM of converting raw MR data to biomass and production values, rather than the traditional method of soil coring. A comparison of MR biomass data to data acquired from a one-time sampling of soil cores is discussed in detail in Section 3.4.3. As a result of this comparison, it was found that FR biomass estimated from MR data were similar to estimates from soil cores, confirming that the PIM is an acceptable means of converting MR data to biomass values and that the data presented in this study is reasonable. Fine root biomass and production estimates from this study are also comparable to values reported by other researchers for boreal species as shown in Table 2.1. Using MR technology at the same BERMS sites used in this study, Steele et al. (1997) found FR biomass values to range from approximately 1.33 to 1.67 Mg ha^{-1} yr^{-1} for jack pine and 1.33 to 1.75 Mg ha^{-1} yr^{-1} for black spruce, while results from this study ranged from 1.35 Mg ha^{-1} yr^{-1} at OJP in 2003 to 2.85 Mg ha^{-1} yr^{-1} at HJP94 in 2006 and 2.09 to 2.86 Mg ha^{-1} yr^{-1} at OBS (Table 3.3). O'Connell et al. (2003) reported FR production estimates of 2.22 Mg ha^{-1} yr^{-1} and Ruess et al. (2003) reported values of approximately 2.28, which are very close to estimates for OBS in this study. Results from this study were as much as five times greater than those reported by Steele et al. (1997) for OA FR biomass (2.18 and 0.43 Mg ha^{-1} yr^{-1}, respectively). In a study of elevated CO_2 effects on FR biomass in Wisconsin, USA, King et al. (2001) reported a mean FR biomass value of 1.32 Mg ha^{-1} for their aspen control plot for roots < 1 mm in diameter using MR. In a comparison of root biomass between MR tubes installed in 2002 for this study and those used by Steele (installed in 1994), Kalyn (2005) suggested that the differences could possibly be attributed to clonal differences in the aspen stand as the two sets of tubes were spaced approximately 150 to 200 m apart. High rates of FR production in 2003 could be due to root proliferation due to root damage during tube installation in 2002 (Burke and Raynal, 1994; Hendrick and Pregitzer, 1996a; Joslin and Wolfe, 1999; Majdi, 1996; Pregitzer et al., 1993). Other possible reasons include influences of the MR tube material itself (Withington et al., 2003), possible alterations to the nutrient status of the mineral soil during tube installation and in subsequent years (Joslin and Wolfe, 1999; Pregitzer et al., 1993; Pregitzer, 1998), air pockets and voids at the soil/tube interface (Gijsman et al., 1991; Phillips et al., 2000; Upchurch and Ritchie, 1983), and the creation of preferential

rooting paths along MR tubes in clayey soils (Ephrath et al., 1999; Upchurch and Ritchie, 1983; Volkmar, 1993). Potential alterations to FR growth in regions immediately surrounding the MR tubes is discussed in greater detail in Chapter 5 of this thesis. The increasing overall trend of FR biomass at the four sites could be due in part to changes in climatic factors as the four years of this study encompassed periods of severe drought and very wet years. A marked decrease in FR biomass between September and October of 2004 was likely the result of a switch between the individuals completing the MR image analysis. This is an example of the idiosyncratic nature of the MR technique where one researcher may say a root is dead and another may think the root has disappeared and removes it from the analysis.

Annual FR production estimates from this study (Table 3.5) are also comparable to those reported by Steele et al. (1997) where FR NPP values were 2.09 and 2.35 Mg ha^{-1} yr^{-1} for black spruce and jack pine, respectively. As with our FR biomass estimates, FR production was found to be much greater in this study at OA compared to the values from Steele (1997) (0.58 Mg ha^{-1} yr^{-1}). Possible reasons for this discrepancy could include clonal differences within the aspen stand. However, compared to mean annual FR NPP estimates from HJP94, OJP, and OBS in this study and other boreal species (Table 2.1), the values for OA are not unreasonably high.

A distinct pattern of intra-annual variability in FR production can be seen in Figure 3.5. Fine root production generally peaks in early summer and declines throughout the fall (Bernier and Robitaille, 2004; Burton et al., 2000; Côté et al., 1998; Hendricks et al., 2006; Joslin et al., 2006; Wells and Eissenstat, 2001; Wells et al., 2002). Some studies have found this annual cycle to be more closely related to the seasonal rise and fall of soil temperature coinciding with aboveground processes such as leaf-out and senescence (McMichael and Quisenberry, 1993; McMichael and Burke, 1996; Pregitzer et al., 2000; Ruess et al., 2003; Steele et al., 1997). Fine root growth is believed to be near zero during the winter months when soil temperatures drop below the threshold for root development (approximately 0 – 7 ºC) and water and nutrient demand of the tree is minimal (Hendrick and Pregitzer, 1996b; McMichael and Burke, 1996; Pregitzer et al., 2000). Similar to the results at OBS in this study, Ruess et al. (2003) found in a study of three Alaskan black spruce stands that root production was delayed by approximately one month compared to early successional floodplain forests due to the thick moss insulating the soil which slowed soil warming. Similar findings regarding delayed root activity at black spruce sites were also reported by Steele et al. (1997) and O'Connell et al. (2003). However, Hendrick and Pregitzer (1992a) and Burke and Raynal (1994) found that in northern

hardwoods, maximum root production occurred in the spring, coinciding with canopy development. This was also observed for OA in this study.

Annual fluctuations in FR production from spring to fall appear to be decreasing in magnitude from 2003 to 2006 (Figure 3.5). As FR production is based on the difference in FR biomass between sampling periods when using the PIM, if measured FR biomass values from MR data become closer to one another between sessions (i.e., dead/disappeared roots are removed from analysis at a similar rate to new roots being recorded), measured production rates effectively decrease. The decrease in magnitude of inter-annual fluctuations in FR production in this study suggests that after four years, FR production could be nearing equilibrium with FR mortality/decomposition rates.

3.4.2 Fine root biomass, production, and soil environmental factors

Soil moisture and soil temperature are strongly related to FR production and biomass (Hogg et al., 2005; McMichael and Quisenberry, 1993; McMichael and Burke, 1996; Noguchi et al., 2007; Pregitzer et al., 2002; Vogt et al., 1996). In a series of correlations and multiple linear regressions in this study (Tables 3.6 and 3.7), it was noted that soil temperature was important at OBS and OA (moisture is not limiting at these sites). Ruess et al. (2003), Steele et al. (1997), and O'Connell et al. (2003) determined that soil temperature had a greater influence on FR growth than soil moisture. Tryon and Chapin (1983) found that the growth of Boreal FR is positively (and exponentially) correlated to increasing soil temperature particularly for aspen. At HJP94, soil moisture was found to be very important along with soil temperature for FR biomass and production estimates. Overall, the regression models derived using soil temperature and moisture, although significant, were not able to explain the variability in FR biomass or production very well as seen by the low model R^2 values in Table 3.7 (with exception of FR biomass at OA with an R^2 = 0.601). Cairns et al. (1997) used seven different predictive variables (age, latitudinal class, soil texture, temperature (T), precipitation (P), T/P ratios, and tree type) to try to estimate root biomass density (RBD). None of these seven factors alone had predictive value in estimating RBD. However, they found that aboveground biomass density (ABD) accounted for 83% of RBD variation. This is why ratios of aboveground shoot biomass to belowground roots are often used to estimate root biomass for C accounting purposes (Mokany et al., 2006). After ABD was accounted for in the study conducted by Cairns et al., the only other factors of the seven tested that had a significant effect on the RBD model were stand age and latitudinal zone.

The results of Cairns et al. (1997) suggests that there may be other factors, whether aboveground or belowground, biotic or abiotic, required to increase the accuracy of the regression models presented in this study as these factors do not work alone but rather interact with each other (Block et al., 2006).

3.4.3 Comparison of MR and SSC estimates of FR biomass

Fine root biomass estimates collected from sequential soil cores and MR data from August 2005 were similar to one another at OJP, OA, and OBS as seen in Figure 3.6. These measurements were done as a follow-up to the work of Kalyn (2005) where 2 mm MR data were compared to soil core data where roots had a 7 mm diameter cut-off. Kalyn (2005) found that using a 7 mm diameter class definition led to FR biomass estimates from soil cores that were 1-6 times greater than those from MR data collected at HJP94, OJP, OA, and OBS. It was only at HJP94 that the large difference in diameter classes did not appear to have an effect on the FR biomass values.

In the current study, HJP94 was the only site that showed significant differences in FR biomass, with a MR estimate nearly four times that of soil coring. The most probable explanation for the MR estimate being much greater than the SSC estimate is the existence of preferential rooting paths along the MR tube (Chapter 4).

The important thing to note from this study is that using a common diameter class cut-off point is crucial when comparing methods. As sequential soil coring is considered the standard in many FR studies, these findings help to validate the use of the PIM with MR in measuring FR biomass.

3.4.4 Distribution of ecosystem biomass carbon and carbon production

Fine root biomass C was found to be a small portion of total ecosystem biomass C, ranging from <1% at OA and OBS to 2% at HJP (Table 3.8). The primary reason for the relatively small contribution of FR to ecosystem biomass C is the large relative amounts of C stored in both the mineral soil and stems. Fine roots are ephemeral by nature and tend to turnover rapidly (Baddeley and Watson, 2005; Bloomfield et al., 1996; Fogel, 1983; Joslin et al., 2006; Majdi et al., 2005; Santantonio and Grace, 1987; Steele et al., 1997; Wells and Eissenstat, 2001). This means that C stored in FR biomass is quickly cycled back into the labile soil C pool. Fine root turnover and longevity will be discussed in further detail in Chapter 4.

Ecosystem C production estimates (Table 3.9) were found to be comparable to total NPP values ranging from 0.52 – 8.68 Mg ha^{-1} yr^{-1} as summarized by Li et al.

(2003) and Gower et al. (2001) for boreal forest ecosystems. Gower et al. (2001) reviewed NPP_T (total NPP) values for 24 boreal forests with complete NPP budgets (Class I) from around the world and calculated an average of 4.24 Mg NPP ha^{-1} yr^{-1}. Total ecosystem NPP in this study ranged from 2.1 Mg ha^{-1} yr^{-1} at HJP94 to 4.8 Mg ha^{-1} yr^{-1} at OA.

Fine root NPP values accounted for a considerable portion of NPP_T for HJP94 and OBS (47 and 54% respectively). These two sites are generally the most active of the four sites (Figures 3.4 and 3.5). Ratios of NPP_B (belowground NPP) to NPP_T for this study, with values of 0.57, 0.36, 0.65, and 0.31 for HJP94, OJP, OBS, and OA, respectively, followed a pattern related to site quality that Gower et al. (1997, 2001) also noted. In two studies regarding jack pine, aspen, and black spruce stands in Saskatchewan and Manitoba, Gower et al. (1997, 2001) reported that aboveground NPP values were consistently higher for deciduous stands compared to conifers as was the case in this study. Gower et al. (2001) found that the ratios of NPP_B to NPP_T are generally greater for evergreen stands (0.36) than for deciduous stands (0.19) which have been attributed to site quality. Similarly, Ruess et al. (1996) found that FR biomass was significantly higher at coniferous stands compared to deciduous stands in the boreal forest of the Alaskan interior. Deciduous forests often have higher soil nutrient levels than coniferous forests. As such, more C is allocated to the aboveground components of the tree. Conversely, the conifer stands allocate more resources to belowground production in response to low soil fertility, low soil temperatures, and extremes in soil moisture (McMichael and Quisenberry, 1993; Ruess et al., 2003).

3.5 Conclusion

Looking at the data presented in this study, we can begin to appreciate the complexity of boreal ecosystems. Fine root biomass estimates were found to have been gradually increasing over the course of four years at each site, indicating that FR biomass production is occurring at a greater rate than FR mortality. Decreasing FR productivity values in combination with this slow biomass accumulation suggest that root dynamics in the vicinity of the MR tubes may be approaching equilibrium. Many studies suggest that one full year is required for the surrounding soil and roots to equilibrate after tube installation. Perhaps the adjustment period required following initial tube installation is longer than previously believed. However, the biomass values that were gathered from soil cores at each site were comparable to those derived from MR data, with the exception of HJP94. The differences at HJP94

were possibly due to the existence of preferential rooting paths along the MR tubes. The consistency between the two methods helps to validate the use of the PIM in converting MR data to biomass as soil coring is the traditional standard used in many FR studies. It would be interesting to see MR data for a longer period of time at these sites. How do FR dynamics change over 5, 10, or even 15 years? How does the balance between FR production and mortality fluctuate over an extended period of time? Studies that run long enough to possibly answer such questions are difficult to put in place due to high costs, consistent training of personnel, and the continuously changing visions of funding agencies.

In this study, FR, while contributing relatively little to total biomass C, were found to be quite important to total ecosystem NPP. The greatest contributions of FR to C production occurred at HJP94 and OBS, which were the two most productive sites in terms of FR biomass production. Belowground NPP values appeared to be greater at the coniferous sites compared to the deciduous OA site, which has been shown in other studies as well. With the large portion of NPP that is allocated to FR systems in the boreal forest, emphasizing research that will improve our knowledge of the specific dynamics of FR is essential. As mentioned above, the need for long term FR studies is crucial. Where does the C that is assimilated into FR go when the roots die? How long does this C remain in the soil? Which forests are the greatest C sinks and which are the sources? How much anthropogenic CO_2 can these forests sequester? These are questions that cannot be answered in the short term, but still need to be answered nonetheless.

3.6 Literature cited

Baddeley, J., and C. Watson. 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant Soil 276:15-22.

Bernier, P.Y., and G. Robitaille. 2004. A plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265:165-173.

Block, R., K. Van Rees, and J. Knight. 2006. A review of fine root dynamics in *Populus* plantations. Agrofor. Syst. 67:73-84.

Bloomfield, J., K. Vogt, and P.M. Wargo. 1996. Tree turnover and senescence, p. 363-381, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half., 2nd ed. Marcel Dekker, New York.

Burke, M.K., and D.J. Raynal. 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135-146.

Burton, A.J., K.S. Pregitzer, and R.L. Hendrick. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia 125:389-399.

Cairns, M.A., S. Brown, E.H. Helmer, and G.A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia 111:1-11.

Côté, B., W.H. Hendershot, J.W. Fyles, A.G. Roy, R. Bradley, P.M. Biron, and F. Courchesne. 1998. The phenology of fine root growth in a maple-dominated ecosystem: relationships with some soil properties. Plant Soil 201:59-69.

Dixon, R.K., A.M. Solomon, S. Brown, R.A. Houghton, M.C. Trexier, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science 263:185-190.

Ephrath, J.E., M. Silberbush, and P.R. Berliner. 1999. Calibration of minirhizotron readings against root length density data obtained from soil cores. Plant Soil 209:201-208.

Falkowski, P., R.J. Scholes, E. Boyle, J. Canadell, D. Canfield, J. Elser, N. Gruber, K. Hibbard, P. Hogberg, S. Linder, F.T. Mackenzie, B. Moore, III, T. Pedersen, Y. Rosenthal, S. Seitzinger, V. Smetacek, and W. Steffen. 2000. The global carbon cycle: a test of our knowledge of Earth as a system. Science 290:291-296.

Field, A. 2005. Discovering Statistics Using SPSS. 2nd ed. Sage Publications Ltd., London, England.

Fogel, R. 1983. Root turnover and productivity of coniferous forests. Plant Soil 71:75-85.

Gijsman, A.J., J. Floris, M. Noordwijk, and G. Brouwer. 1991. An inflatable minirhizotron system for root observations with improved soil/tube contact. Plant Soil 134:261-269.

Gill, R.A., and R.B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147:13-31.

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, and S.J. Steele. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102:29,029-29,041.

Gower, S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder, and C. Wang. 2001. Net primary production and carbon allocation patterns of Boreal forest ecosystems. Ecol. Appl. 11:1395-1411.

Hendrick, R.L., and K.S. Pregitzer. 1992a. The demography of fine roots in a northern hardwood forest. Ecology 73:1094-1104.

Hendrick, R.L., and K.S. Pregitzer. 1992b. Spatial variation in tree root distribution and growth associated with minirhizotrons. Plant Soil 143:283-288.

Hendrick, R., and K.S. Pregitzer. 1996a. Applications of minirhizotrons to understand root function in forests and other natural ecosystems. Plant Soil 185:293-304.

Hendrick, R.L., and K.S. Pregitzer. 1996b. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. J Ecol. 84:167-176.

Hendricks, J.J., R.L. Hendrick, C.A. Wilson, R.J. Mitchell, S.D. Pecot, and D. Guo. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J. Ecol. 94:40-57.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting inter-annual variation in growth of Western Canadian aspen forests during 1951-2000. Can. J. For. Res. 35:610-622.

Howard, E.A., S.T. Gower, J.A. Foley, and C.J. Kucharik. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Glob. Change Biol. 10:1267-1284.

Johnson, M.G., D.T. Tingey, D.L. Phillips, and M.J. Storm. 2001. Advancing fine root research with minirhizotrons. Env. Exp. Bot. 45:263-289.

Joslin, J.D., and M.H. Wolfe. 1999. Disturbances during minirhizotron installation can affect root observation data. Soil Sci. Soc. Am. J. 63:218-221.

Joslin, J.D., J.B. Gaudinski, M.S. Torn, W.J. Riley, and P.J. Hanson. 2006. Fine-root turnover patterns and their relationship to root diameter and soil depth in a 14C-labeled hardwood forest. New Phytol. 172:523-535.

Kalyn, A. 2005. Fine root dynamics and belowground carbon-cycling in the boreal forests of Saskatchewan., University of Saskatchewan, Saskatoon, SK, Canada.

King, J.S., K.S. Pregitzer, D.R.Zak, J. Sober, J.G. Isebrands, R.E. Dickson, G.R. Hendrey, and D.F. Karnosky. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. Oecologia 128:237-250.

Lal, R., J. Kimble, and R. Follett. 1997. Land use and soil C pools in terrestrial ecosystems. *In* pp 1 – 10. R. Lal, et al. eds. Management of carbon sequestration in soil. CRC Press, Boca Raton, FL, USA.

Li, Z., W.A. Kurz, M.J. Apps, and S.J. Beukema. 2003. Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Can. J. For. Res. 33:126-136.

Majdi, H. 1996. Root sampling methods - applications and limitations of the minirhizotron technique. Plant Soil 185:255-258.

Majdi, H., K. Pregitzer, A.-S. Morén, J.-E. Nylund, and G. I. Ågren. 2005. Measuring fine root turnover in forest ecosystems. Plant Soil 276:1-8.

Malhi, Y., D.D. Baldocch, and P.G. Jarvis. 1999. The carbon balance of tropical, temperate, and boreal forests. Plant Cell Environ. 22:715-740.

McMichael, B.L., and J.E. Quisenberry. 1993. The impact of the soil environment on the growth of root systems. Env. Exp. Bot. 33:53-61.

McMichael, B.L., and J.J. Burke. 1996. Temperature effects on root growth *In* pp 383 – 396. Waisel, Y., et al. eds. Plant roots: the hidden half. 2nd ed. Marcel Dekker, Inc., New York, NY, USA.

Mokany, K., R.J. Raison, and A.S. Prokushkin. 2006. Critical analysis of root : shoot ratios in terrestrial biomes. Glob. Change Biol. 12:84-96.

Moore, T.R. 1996. The carbon budget of the boreal forests: reducing the uncertainty. *In* A.I. Breymeyer, et al., eds. Global change: effects on coniferous forests and grasslands. pp 17 – 36. John Wiley and Sons Ltd., Chichester, England.

Noguchi, K., B. Konôpka, T. Satomura, S. Kaneko, and M. Takahashi. 2007. Biomass and production of fine roots in Japanese forests. J. For. Res. 12:83-95.

O'Connell, K.E.B., S.T. Gower, and J.M. Norman. 2003. Comparison of net primary production and light-use dynamics of two Boreal black spruce forest communities. Ecosystems 6:236-247.

Pennock, D.J. 2004. Designing field studies in soil science. Can. J. Soil Sci. 84:1-10

Peterman, R.M.. 1990. Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci.. 47:2-15.

Phillips, D.L., M.G. Johnson, D.T. Tingey, C. Biggart, R.S. Nowak, and J.C. Newsom. 2000. Minirhizotron installation in sandy, rocky soils with minimal soil disturbance. Soil Sci. Soc. Am. J. 64:761-764.

Pregitzer, K.S., R.L. Hendrick, and R. Fogel. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytol. 125:575-580.

Pregitzer, K.S., J.S. King, A.J. Burton, and S.E. Brown. 2000. Responses of tree fine roots to temperature. New Phytol. 147:105-115.

Pregitzer, K.S., J.L. DeForest, A.J. Burton, M.F. Allen, R.W. Ruess, and R.L. Hendrick. 2002. Fine root architecture of nine North American trees. Ecol. Monogr. 72:293-309.

Pregitzer, K.S., Laskowski, M. J., Burton, A. J., Lessard, V. C., Zak, D. R. 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol. 18:665-670.

Ruess, R.W., K. Van Cleve, J. Yarie, and L.A. Vierek. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can. J. For. Res. 26:1326-1336.

Ruess, R.W., R.L. Hendrick, A.J. Burton, K.S. Pregitzer, B. Sveinbjornsson, A. M.F., and G.E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol. Monogr. 73:643-662.

Santantonio, D., and J.C. Grace. 1987. Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Can. J. For. Res. 17:900-908.

Schindler, D.W. 1999. Carbon cycling: The mysterious missing sink. Nature 398:105-107.

Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17:577-587.

Theede, A.D. 2007. Biometric and eddy-covariance estimates of ecosystem carbon storage at two Boreal forest stands in Saskatchewan 1994-2004, University of Saskatchewan, Saskatoon, Saskatchewan.

Tryon, P.R. 1983. Temperature control over root growth and root biomass in taiga forest trees. Can. J. For. Res. 13:827-833.

Upchurch, D.R., and J.T. Ritchie. 1983. Root observations using a video recording system in mini-rhizotrons. Agron. J. 75:1009-1015.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. 14:20-26.

Vogt, K.A., D.J. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 200:71-89.

Vogt, K.A., D.J. Vogt, P.A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159-219.

Volkmar, K.M. 1993. A comparison of minirhizotron techniques for estimating root length density in soils of different bulk densities. Plant Soil 157:239-245.

Wells, C.E., and D.M. Eissenstat. 2001. Marked differences in survivorship among apple roots of different diameters. Ecology 82:882-892.

Wells, C.E., D.M. Glenn, and D.M. Eissenstat. 2002. Changes in the risk of fine-root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). Am. J. Bot. 89:79-87.

Withington, J.M., A.D. Elkin, B. Bulaj, J. Olesinski, K.N. Tracy, T.J. Bouma, J. Oleksyn, L.J. Anderson, J. Modrzynski, P.B. Reich, and D.M. Eissenstat. 2003. The impact of material used for minirhizotron tubes for root research. New Phytol. 160:533-544.

4 FINE ROOT BIOMASS DISTRIBUTION, PRODUCTION, AND LONGEVITY OF DIFFERENT ROOT DIAMETER CLASSES IN THE BOREAL FOREST OF SASKATCHEWAN

4.1 Introduction

Fine roots (FR) play an important role in forest systems as the physical link between trees and soil resources. The relatively rapid turnover rates associated with FR (as opposed to larger, woody, structural roots) make them very important to the biogeochemical cycles within forest systems. It has been estimated that FR turnover is more than an order of magnitude greater than the turnover of aboveground litterfall in Boreal Forests of Alaska (Ruess et al., 2005). This large amount of belowground root activity has great implications in global climate change studies making use of carbon (C) cycling models in the Boreal Forest and other forest systems. However, due to the inherent difficulties in root studies, large knowledge gaps still exist regarding the dynamic nature of FR production, longevity, and biomass distribution.

With advances in FR research over the past few years, a number of researchers have begun to question the practice of using a single, arbitrary diameter class (usually 1 – 2 mm) as the definition of a FR (Majdi et al., 2005; Satomura et al., 2007; Wells and Eissenstat, 2001). This generalized diameter class interval makes the assumption that all FR are physiologically and structurally the same. Small white first-order roots have been associated primarily with nutrient and water uptake while larger branched woody roots may also provide stability, transport, and storage along with further lateral root production (Eissenstat et al., 2000a). Further subdivision of the large 1 – 2 mm diameter class into smaller diameter classes, (i.e., using 0.1 mm intervals between classes), may provide researchers with further insight into the dynamics of FR growth in various ecological systems by enabling them to analyze FR parameters at a smaller scale.

Another critical factor in many FR studies is soil depth. Fine root biomass, turnover, and longevity have been known to vary greatly throughout the soil profile (Baddeley and Watson, 2005; Brunner and Godbold, 2007; Wells and Eissenstat, 2001). Approximately 86% of FR biomass in the boreal forest is located in the upper 30 cm of soil (Jackson et al., 1996). A number of studies have found that root lifespan is greater for roots at depth as compared to those nearer the surface (Baddeley and Watson, 2005; Joslin et al., 2006; Wells and Eissenstat, 2001).

The objective of this study was to measure FR biomass, production, longevity, and turnover for six root diameter classes that are < 2 mm in diameter for different soil depths in four boreal ecosystems. It was hypothesized that FR biomass and longevity would increase with increasing soil depth (positive relationship), and that FR production and turnover would decrease with increasing soil depth (negative relationship).

4.2 Materials and methods

4.2.1 Site Descriptions

The four sites used in this study include a young jack pine (HJP94) and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands located in the Boreal Forest of northern Saskatchewan, Canada. The sites are part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) study north of Prince Albert, SK. More detail on each of these sites can be found in Section 3.2.1 and Table 3.1 in Chapter 3 of this thesis.

4.2.2 Minirhizotron data collection and processing

Digital images were collected from nine minirhizotron (MR) tubes at each of the four research sites on a monthly basis from May to September in 2003 – 2006. MR data for each of the four sites for 2003 and 2004 were collected by Kalyn (2005). The MR tubes were installed during the summer of 2002 and were left to settle for a year before sampling commenced. The tubes were arranged in three banks of three tubes in a nested design, with each bank representing an individual nest (Hendrick and Pregitzer, 1992a). Minirhizotron images for all tubes at each of the four sites were truncated at a vertical depth of 40 cm (54 images) as this is the maximum depth attained by the shallowest tube at the OA site.

Image analysis was performed using RooTracker root analysis software (Version 2.0.3b1, Duke University, NC, USA). Root data collected during image analysis in RooTracker was divided into six diameter classes (0.01 − 0.1, 0.1 − 0.2, 0.2 − 0.3, 0.3 − 0.5, 0.5 − 1.0 and 1.0 − 2.0 mm) based on those used by Wells and Eissenstat (2001). Roots that were equal to class endpoint were assigned to the next larger class. To investigate differences in biomass, production, and longevity with soil depth, the RooTracker data were also divided into depths of 0 – 20 and 20 – 40 cm. For the purposes of this study, the overall depth range of approximately 40 cm that was common for all data for all four sites was divided into 20 cm increments

rather than 10 cm increments to ease the handling of the large dataset when looking at six diameter classes. Depth intervals in 20 cm increments were also used by Gill et al. (2002) in their study of blue grama root longevity and turnover. Fine root biomass and production values were calculated from the RooTracker output data with the plane intersect method (PIM) proposed by Bernier and Robitaille (2004) using SAS (Version 9.1, SAS Institute Inc, Cary, NC, USA) and averaged over four years. Although FR production and biomass can fluctuate from year to year, this study assumed that the effects of extreme fluctuations would be minimized if the data was averaged between the years. A more detailed description of the MR system and image and data analysis can be found in Section 3.2.2 in Chapter 3.

4.2.3 Calculation of fine root longevity and turnover

There are a number of ways in which FR longevity and turnover can be calculated (Satomura et al., 2007). For the purposes of this study, FR turnover (yr^{-1}) (T_{fr}) was estimated with Eq. [4.1] using a ratio of mean annual FR NPP (NPP_{fr}) to mean annual FR biomass (BM_{fr}) (Block, 2004; Chen et al., 2004; Gill and Jackson, 2000; Kalyn, 2005; Ostonen et al., 2005; Satomura et al., 2007). Mean FR biomass was used in place of the maximum or minimum values described in some studies in order to reduce variation during periods of high and low vegetative production (Ostonen et al., 2005).

$$T_{fr} = \frac{NPP_{fr}}{BM_{fr}} \quad [4.1]$$

Fine root longevity (yr) (L_{fr}) was calculated as the inverse of FR turnover using Eq. [4.2] (Burton et al., 2000; Chen et al., 2004; Majdi and Andersson, 2005; Ostonen et al., 2005; Satomura et al., 2007). Fine root turnover and longevity estimates were calculated for each of the six root diameter classes and two soil depth ranges discussed in Section 4.2.2 above.

$$L_{fr} = \frac{1}{T_{fr}} \quad [4.2]$$

4.2.4 Statistical analysis

The basic plot layout of this study was a nested design with each bank of MR tubes considered an independent nest (Hendrick and Pregitzer, 1992a). Statistical analyses in this study were completed using a combination of SAS and SPSS (SPSS for Windows, Release 14.0.0, SPSS Inc, Chicago, IL, USA) statistical software packages. Initial application of the PIM to the raw MR data from RooTracker was

done using SAS (Bernier and Robitaille, 2004). Data output from the PIM were then statistically analyzed in SPSS. Differences in FR biomass, production, turnover and longevity between diameter classes for each soil depth were tested using Ryan-Einot-Gabriel-Welsch *Q* (REGWQ) and Dunnett's T3, depending on the results of Levene's test of homogeneity of variance in one-way ANOVA in SPSS ($\alpha = 0.10$). Both the REGWQ and Dunnett's T3 tests maintain tight control of Type I error while maintaining good statistical power (Field, 2005). Differences in FR biomass, production, turnover, and longevity between soil depths for each diameter class were tested using paired samples T-tests in SPSS ($\alpha = 0.10$). Values for FR biomass and production were transformed to fit a normal distribution using square root and natural log transformations, respectively. Fine root turnover and longevity values were found to be normally distributed using the Kolmogorov-Smirnov goodness-of-fit test.

4.3 Results

4.3.1 Fine root biomass and production

Approximately 85, 90, 96, and 96% of FR measured in this study were found to be less than 0.5 mm in diameter with median diameters of 0.250 ± 0.237, 0.225 ± 0.208, 0.175 ± 0.149 and 0.150 ± 0.149 mm at HJP94, OJP, OA, and OBS, respectively (Figure 4.1). The total number of roots observed at each site was much lower at HJP94 and OJP (4905 and 3591) compared to OA and OBS (13364 and 16240). Fine root diameter class significantly affected FR biomass at all four sites for a depth interval of 0 – 40 cm with a general pattern of increasing biomass with an increase in root diameter (Table 4.1). Diameter class did not significantly influence estimates of FR production to a depth of 40 cm (Table 4.2). For depth intervals of 0 – 20 and 20 – 40 cm, diameter class had no effect on FR biomass and production with the exception of FR biomass at OA from 20 – 40 cm (Tables 4.1 and 4.2). When FR biomass estimates for each diameter class were compared between depth intervals of 0 – 20 and 20 – 40 cm using paired-means T-tests, significant differences were found at OJP (0.01 – 0.1 and 1.0 – 2.0 mm diameter classes) and at OBS (0.01 – 0.1, and 0.3 – 0.5 mm diameter classes) with FR biomass being greater for the 0 – 20 cm interval, and at HJP94 (0.01 – 0.1 and 0.3 – 0.5 mm diameter classes) and the at OA (0.3 – 0.5 mm diameter class) with biomass being greater for the 20 – 40 cm interval, (Table 4.3). A comparison of FR production between depth intervals of 0 – 20 and 20 – 40 cm found significant differences at OJP (0.3 – 0.5, and 1.0 – 2.0 mm diameter classes), OA (1.0 – 2.0 mm diameter class), and OBS (0.01 – 0.1, 0.3 – 0.5, and 1.0 –

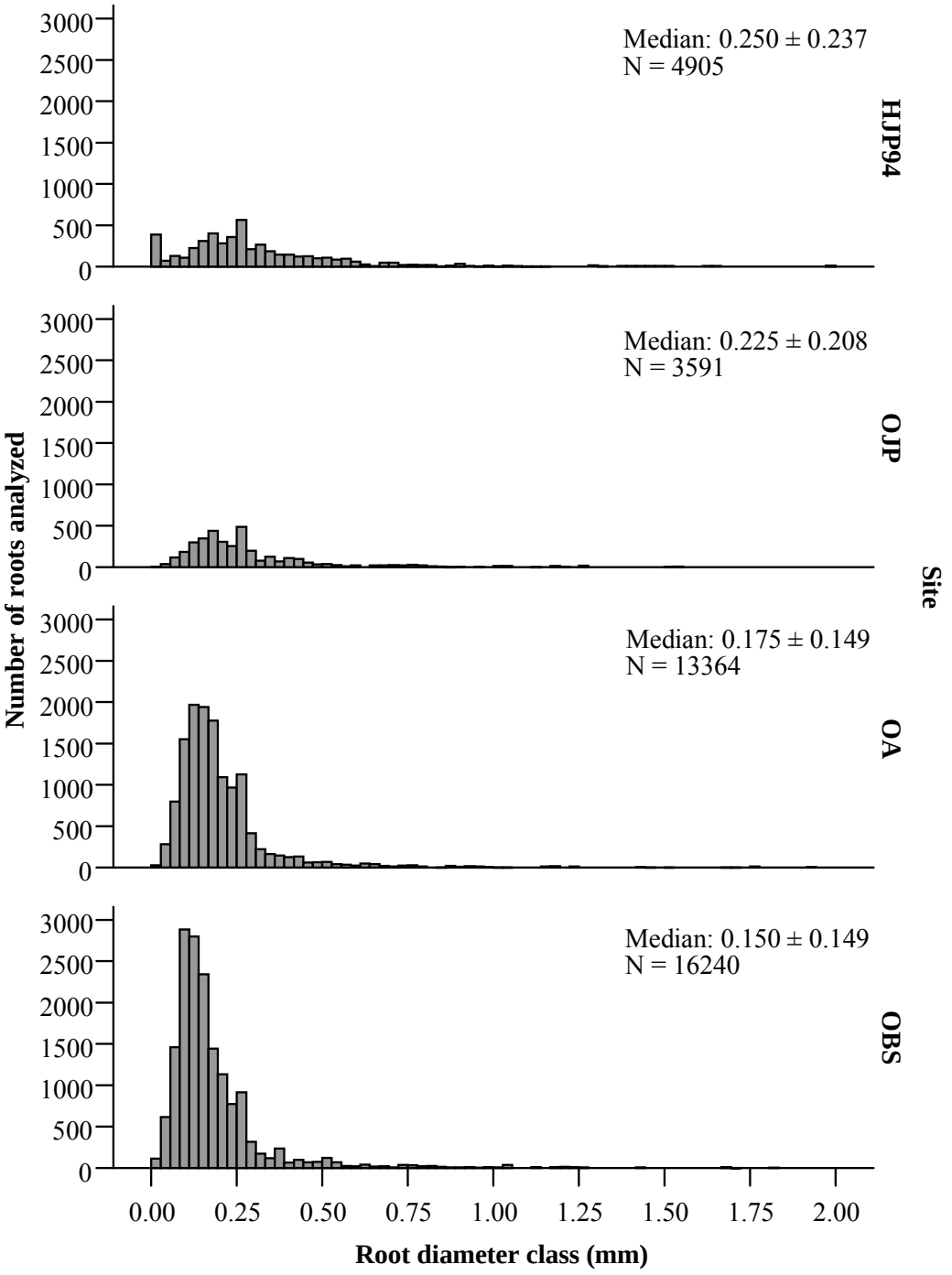

Figure 4.1: Fine root diameter distributions for all roots measured using minirhizotrons to a vertical depth of 40 cm for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan for 2003 to 2006 combined.

Table 4.1: Mean fine root biomass for vertical depths of 0 – 20, 20 – 40, and 0 – 40 cm by root diameter class for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006. Values in parentheses represent 1 SD (N=4).

Diameter Class	Mean fine root biomass			
	HJP94	OJP	OA	OBS
	---------- Mg ha^{-1} ----------			
			0 – 20 cm	
0.01 – 0.1	0.125 (0.071) a†	0.202 (0.086) a	0.243 (0.068) a	0.213 (0.055) a
0.1 – 0.2	0.762 (0.763) a	0.569 (0.373) a	0.333 (0.142) a	0.604 (0.217) a
0.2 – 0.3	0.845 (0.179) a	0.932 (0.168) a	0.419 (0.069) a	0.904 (0.094) a
0.3 – 0.5	0.182 (0.094) a	0.214 (0.084) a	0.170 (0.052) a	0.474 (0.095) a
0.5 – 1.0	1.10 (0.952) a	0.902 (0.644) a	0.334 (0.133) a	1.24 (0.476) a
1.0 – 2.0	1.76 (0.458) a	1.43 (0.298) a	0.779 (0.093) a	1.46 (0.118) a
			20 – 40 cm	
0.01 – 0.1	0.240 (0.129) a	0.094 (0.043) a	0.350 (0.096) b	0.099 (0.021) a
0.1 – 0.2	0.292 (0.235) a	0.185 (0.151) a	0.642 (0.433) ab	0.491 (0.439) a
0.2 – 0.3	0.986 (0.100) a	0.328 (0.050) a	1.19 (0.059) ab	0.277 (0.120) a
0.3 – 0.5	0.260 (0.118) a	0.159 (0.063) a	0.843 (0.216) ab	0.176 (0.034) a
0.5 – 1.0	0.577 (0.328) a	0.347 (0.177) a	0.818 (0.283) ab	0.385 (0.187) a
1.0 – 2.0	1.13 (0.063) a	0.630 (0.055) a	2.13 (0.043) a	0.571 (0.107) a
			0 – 40 cm	
0.01 – 0.1	0.018 (0.000) d	0.010 (0.000) d	0.027 (0.000) c	0.056 (0.004) c
0.1 – 0.2	0.265 (0.011) c	0.215 (0.006) c	0.598 (0.014) b	0.777 (0.098) b
0.2 – 0.3	0.766 (0.031) c	0.463 (0.016) bc	0.723 (0.017) b	0.689 (0.053) b
0.3 – 0.5	1.73 (0.022) b	0.739 (0.008) b	0.624 (0.027) b	0.729 (0.027) b
0.5 – 1.0	3.02 (0.076) ab	1.20 (0.007) a	0.956 (0.002) b	1.22 (0.014) b
1.0 – 2.0	4.30 (0.083) a	2.93 (0.129) a	1.66 (0.014) a	2.76 (0.068) a

† For each depth, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using Dunnett's T3 for simple one-way ANOVA.

Table 4.2: Mean annual fine root production for vertical depths of 0 – 20, 20 – 40, and 0 – 40 cm by root diameter class for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006. Values in parentheses represent 1 SD (N=4).

Diameter Class	Mean fine root production			
	HJP94	OJP	OA	OBS
	---------- Mg ha^{-1} yr^{-1} ----------			
		0 – 20 cm		
0.01 – 0.1	0.027 (0.037) a†	0.044 (0.042) a	0.080 (0.076) a	0.086 (0.059) a
0.1 – 0.2	0.094 (0.155) a	0.044 (0.077) a	0.029 (0.031) a	0.059 (0.064) a
0.2 – 0.3	0.044 (0.047) a	0.078 (0.060) a	0.028 (0.033) a	0.088 (0.076) a
0.3 – 0.5	0.025 (0.029) a	0.047 (0.041) a	0.034 (0.025) a	0.098 (0.061) a
0.5 – 1.0	0.077 (0.143) a	0.193 (0.280) a	0.017 (0.018) a	0.176 (0.182) a
1.0 – 2.0	0.043 (0.044) a	0.031 (0.021) a	0.054 (0.030) a	0.052 (0.035) a
		20 – 40 cm		
0.01 – 0.1	0.052 (0.059) a	0.007 (0.008) a	0.026 (0.017) a	0.042 (0.033) a
0.1 – 0.2	0.029 (0.037) a	0.003 (0.006) a	0.035 (0.055) a	0.017 (0.019) a
0.2 – 0.3	0.041 (0.027) a	0.036 (0.040) a	0.065 (0.079) a	0.070 (0.138) a
0.3 – 0.5	0.019 (0.019) a	0.017 (0.016) a	0.021 (0.015) a	0.036 (0.025) a
0.5 – 1.0	0.031 (0.028) a	0.020 (0.034) a	0.009 (0.010) a	0.046 (0.071) a
1.0 – 2.0	0.024 (0.016) a	0.013 (0.016) a	0.011 (0.009) a	0.012 (0.015) a
		0 – 40 cm		
0.01 – 0.1	0.105 (0.109) a	0.041 (0.034) a	0.143 (0.109) a	0.106 (0.066) a
0.1 – 0.2	0.165 (0.175) a	0.045 (0.073) a	0.075 (0.093) a	0.134 (0.108) a
0.2 – 0.3	0.105 (0.095) a	0.100 (0.048) a	0.126 (0.020) a	0.101 (0.097) a
0.3 – 0.5	0.055 (0.062) a	0.058 (0.052) a	0.054 (0.038) a	0.119 (0.073) a
0.5 – 1.0	0.140 (0.141) a	0.223 (0.338) a	0.040 (0.038) a	0.193 (0.177) a
1.0 – 2.0	0.072 (0.053) a	0.038 (0.026) a	0.075 (0.026) a	0.059 (0.042) a

† For each depth range, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using Dunnett's T3 for simple one-way ANOVA.

Table 4.3: Paired-means t-tests comparing mean fine root biomass estimates from minirhizotron data for depths of 0 – 20 cm and 20 – 40 cm at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 combined. Positive *t* values mean that FR biomass values for 0 – 20 cm depth intervals are greater while negative *t* values mean that biomass values for 20 – 40 cm depth intervals are greater

Site	Diameter Class	Mean Difference	df	*t*	Sig. (2-tailed)	*r*
HJP94	0.01 − 0.1	-0.136	3	-2.75	0.071*	0.846
	0.1 – 0.2	0.467	3	0.920	0.425	0.469
	0.2 – 0.3	-0.074	3	-0.808	0.478	0.423
	0.3 – 0.5	-0.083	3	-4.26	0.024*	0.926
	0.5 – 1.0	0.289	3	1.39	0.258	0.626
	1.0 – 2.0	0.262	3	1.19	0.320	0.566
OJP	0.01 − 0.1	0.141	3	2.83	0.066*	0.853
	0.1 – 0.2	0.432	3	1.35	0.270	0.615
	0.2 – 0.3	0.536	3	1.64	0.199	0.688
	0.3 – 0.5	0.063	3	1.58	0.212	0.674
	0.5 – 1.0	0.361	3	1.87	0.159	0.734
	1.0 – 2.0	0.405	3	2.40	0.096*	0.811
OA	0.01 − 0.1	-0.099	3	-0.706	0.531	0.377
	0.1 – 0.2	-0.024	3	-0.064	0.953	0.037
	0.2 – 0.3	-0.171	3	-0.422	0.701	0.237
	0.3 – 0.5	-0.505	3	-4.13	0.026*	0.922
	0.5 – 1.0	-0.100	3	-0.260	0.812	0.148
	1.0 – 2.0	-0.213	3	-0.408	0.711	0.229
OBS	0.01 − 0.1	0.146	3	3.00	0.058*	0.866
	0.1 – 0.2	0.076	3	0.498	0.653	0.276
	0.2 – 0.3	0.556	3	2.02	0.137	0.759
	0.3 – 0.5	0.269	3	3.34	0.045*	0.888
	0.5 – 1.0	0.648	3	1.42	0.250	0.635
	1.0 – 2.0	0.642	3	1.69	0.190	0.698

* denotes significance at $\alpha = 0.1$

2.0 mm diameter classes) with FR production being greater for the 0 – 20 cm depth interval, and at a depth interval of 20 – 40 cm in the 0.01 – 0.1 mm diameter class at HJP94 (Table 4.4).

4.3.2 Fine root longevity and turnover

Fine root longevity in this study ranged from approximately 1.15 ± 0.514 to 9.83 ± 8.57 years for the 0 – 20 cm depth and 1.54 ± 0.58 to 22.5 ± 20.0 years for the depth interval of 20 – 40 cm (Table 4.5). The largest diameter class in this study (1.0 – 2.0 mm) had a significantly longer lifespan than the other five diameter classes at OA for the 0 – 20 and 0 – 40 cm soil depth intervals. Significant differences in FR longevity between diameter classes were also found at HJP94 for a 20 – 40 cm depth. When individual diameter classes were compared between depths of 0 – 20 and 20 – 40 cm for each site across all four years of the study, differences were found at HJP94, OA, and OBS (Table 4.6). The significant differences were found for diameter classes of 0.5 – 1.0 mm at HJP94, 0.01 – 0.1, 0.1 – 0.2, and 0.2 – 0.3 mm at OA, and 0.1 – 0.2 mm at OBS. No significant differences in FR longevity between depth intervals were noted at OJP.

Fine root turnover was greatest at OBS with an estimate of 1.05 ± 0.471 yr^{-1} for the 0 – 20 cm soil depth (Table 4.7). Average turnover values across all root diameters to a 40 cm depth were 0.497, 0.546, 0.713, and 0.802 yr^{-1} for HJP94, OJP, OA, and OBS, respectively. Turnover was low at OA for the 20 – 40 cm depth, ranging from 0.100 to 0.181 yr^{-1} which coincides with the largest longevity estimates. Significant differences in FR turnover between diameter classes were found at OA for depths of 0 – 20 and 0 – 40 cm and at OJP for a 0 – 40 cm depth. A general trend of decreasing FR turnover with increasing soil depth was found when individual diameter classes were compared between the two soil depths (Table 4.8). Significant differences in FR turnover between sampling depths were found at OA for all diameter classes. Significant differences in FR turnover were found at HJP94 for 0.01 – 0.1, 0.2 – 0.3, and 0.5 – 1.0 mm diameter classes and at OJP for the 0.3 – 0.5 mm diameter class.

The one-way ANOVA results for all three soil depth increments at each site (HJP94, OJP, OA, and OBS) for FR biomass, production, turnover, and longevity can be found in Table D.1 in Appendix D.

Table 4.4: Paired-means t-tests comparing mean fine root production estimates from minirhizotron data for depths of 0 – 20 cm and 20 – 40 cm at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 combined. Positive *t* values mean that FR biomass values for 0 – 20 cm depth intervals are greater while negative *t* values mean that biomass values for 20 – 40 cm depth intervals are greater

Site	Diameter Class	Mean Difference	df	*t*	Sig. (2-tailed)	*r*
HJP94	0.01 − 0.1	-0.032	3	-2.85	0.065*	0.855
	0.1 – 0.2	0.134	3	1.59	0.211	0.677
	0.2 – 0.3	0.003	3	0.176	0.871	0.102
	0.3 – 0.5	0.006	3	1.14	0.337	0.550
	0.5 – 1.0	0.046	3	0.725	0.521	0.386
	1.0 – 2.0	0.019	3	1.03	0.379	0.511
OJP	0.01 − 0.1	0.038	3	1.80	0.169	0.721
	0.1 – 0.2	0.041	3	1.04	0.375	0.515
	0.2 – 0.3	0.042	3	0.950	0.412	0.481
	0.3 – 0.5	0.030	3	2.37	0.099*	0.807
	0.5 – 1.0	0.173	3	1.20	0.316	0.569
	1.0 – 2.0	0.018	3	2.51	0.087*	0.823
OA	0.01 − 0.1	0.054	3	1.49	0.234	0.652
	0.1 – 0.2	-0.007	3	-0.495	0.655	0.275
	0.2 – 0.3	-0.037	3	-1.03	0.379	0.511
	0.3 – 0.5	0.013	3	2.12	0.124	0.774
	0.5 – 1.0	0.008	3	1.85	0.162	0.730
	1.0 – 2.0	0.043	3	2.38	0.098*	0.809
OBS	0.01 − 0.1	0.044	3	2.55	0.084*	0.827
	0.1 – 0.2	0.042	3	1.856	0.160	0.731
	0.2 – 0.3	0.018	3	0.433	0.694	0.243
	0.3 – 0.5	0.062	3	2.73	0.072*	0.844
	0.5 – 1.0	0.130	3	1.24	0.304	0.582
	1.0 – 2.0	0.040	3	2.91	0.062*	0.859

* denotes significance at $\alpha = 0.1$

Table 4.5: Mean fine root longevity for vertical depths of 0 – 20, 20 – 40, and 0 – 40 cm by root diameter class for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006. Values in parentheses represent 1 SD (N=4).

Diameter Class	Mean fine root longevity			
	HJP94	OJP	OA	OBS
	---------- yr ----------			
		0 – 20 cm		
0.01 – 0.1	2.69 (0.314) a†	2.22 (0.528) a	1.44 (0.491) b‡	1.23 (0.327) a
0.1 – 0.2	1.73 (0.493) a	1.67 (0.427) a	1.19 (0.450) b	1.16 (0.662) a
0.2 – 0.3	1.98 (0.941) a	1.66 (0.780) a	1.15 (0.514) b	1.40 (0.951) a
0.3 – 0.5	2.61 (1.33) a	2.13 (0.987) a	1.68 (1.07) b	1.52 (0.917) a
0.5 – 1.0	2.74 (2.16) a	4.02 (2.77) a	2.80 (1.32) b	2.26 (1.40) a
1.0 – 2.0		2.01 (1.01) a	9.83 (8.57) a	1.80 (0.000) a
		20 – 40 cm		
0.01 – 0.1	4.43 (3.75) ab		11.7 (5.15) a	1.66 (0.54) a
0.1 – 0.2	2.10 (0.90)b	2.19 (1.05) a	7.31 (4.44) a	1.64 (0.83) a
0.2 – 0.3	2.46 (1.43)b	11.1 (18.6) a	8.43 (6.20) a	3.06 (3.03) a
0.3 – 0.5	3.44 (1.64)ab	4.20 (2.43) a	18.1 (23.2) a	1.90 (1.85) a
0.5 – 1.0	5.34 (2.62)a	1.61 (0.25) a	22.5 (20.0) a	1.54 (0.58) a
1.0 – 2.0	7.14 (0.00)a			
		0 – 40 cm		
0.01 – 0.1	2.27 (1.03) a	2.83 (1.02) a	1.40 (0.345) b	1.25 (0.343) a
0.1 – 0.2	1.83 (0.862) a	1.61 (0.354) a	1.29 (0.571) b	1.21 (0.708) a
0.2 – 0.3	2.20 (1.30) a	1.38 (0.201) a	1.25 (0.565) b	1.36 (0.842) a
0.3 – 0.5	2.84 (1.37) a	1.58 (0.270) a	1.55 (1.10) b	1.54 (1.02) a
0.5 – 1.0	3.26 (2.46) a	2.37 (0.732) a	2.49 (1.34) b	2.43 (1.98) a
1.0 – 2.0	3.92 (1.47) a	5.89 (6.80) a	16.4 (14.9) a	1.82 (0.031) a

† For each depth range, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using simple one-way ANOVA. Differences were tested using Dunnett's T3 post-hoc test for unequal variances.

‡ Differences in fine root longevity values between diameter classes at OA for a 0 – 20 cm depth range were tested using the REGWQ post-hoc test for equal variances.

Table 4.6: Paired-means t-tests comparing mean fine root longevity estimates from minirhizotron data for depths of 0 – 20 cm and 20 – 40 cm at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 combined. Results were not reported for diameter classes that did not have roots present at both depths. Positive *t* values mean that FR longevity values for 0 – 20 cm depth intervals are greater while negative *t* values mean that longevity values for 20 – 40 cm depth intervals are greater

Site	Diameter Class	Mean Difference	df	*t*	Sig. (2-tailed)	*r*
HJP94	0.01 − 0.1	8.02	3	0.543	0.684	0.299
	0.1 – 0.2	-0.366	3	-1.50	0.230	0.655
	0.2 – 0.3	-0.468	3	-1.41	0.253	0.631
	0.3 – 0.5	-0.839	3	-1.46	0.239	0.645
	0.5 – 1.0	-2.60	3	-8.55	0.003*	0.980
	1.0 – 2.0					
OJP	0.01 − 0.1					
	0.1 – 0.2	-0.515	3	-0.887	0.441	0.456
	0.2 – 0.3	-9.40	3	-0.984	0.398	0.494
	0.3 – 0.5	-2.07	3	-1.481	0.235	0.650
	0.5 – 1.0	1.24	3	1.15	0.456	0.553
	1.0 – 2.0					
OA	0.01 − 0.1	1.34	3	5.26	0.013*	0.950
	0.1 – 0.2	1.01	3	3.81	0.032*	0.910
	0.2 – 0.3	0.973	3	3.122	0.052*	0.874
	0.3 – 0.5	1.54	3	2.62	0.079*	0.834
	0.5 – 1.0	2.69	3	3.271	0.082*	0.884
	1.0 – 2.0					
OBS	0.01 − 0.1	-4.34	3	-2.01	0.137	0.758
	0.1 – 0.2	-0.483	3	-3.881	0.030*	0.913
	0.2 – 0.3	-1.66	3	-1.02	0.384	0.507
	0.3 – 0.5	-0.271	3	-0.625	0.596	0.339
	0.5 – 1.0	0.038	3	0.116	0.918	0.067
	1.0 – 2.0					

* denotes significance at $\alpha = 0.1$

Table 4.7: Mean fine root turnover for vertical depths of 0 – 20 and 20 – 40 cm by root diameter class for four BERMS boreal forest sites, including a harvested jack pine stand (HJP94), and mature jack pine (OJP), aspen (OA), and black spruce (OBS) stands in northern Saskatchewan from 2003 to 2006. Values in parentheses represent 1 SD (N=4).

Diameter Class	Mean fine root turnover			
	HJP94	OJP	OA	OBS
	---------- yr^{-1} ----------			
		0 – 20 cm		
0.01 – 0.1	0.375 (0.038) a†	0.471 (0.119) a	0.761 (0.256) ab‡	0.857 (0.215) a
0.1 – 0.2	0.621 (0.210) a	0.630 (0.169) a	0.964 (0.462) a	1.05 (0.471) a
0.2 – 0.3	0.602 (0.275) a	0.719 (0.334) a	0.987 (0.369) a	0.940 (0.497) a
0.3 – 0.5	0.492 (0.297) a	0.549 (0.237) a	0.757 (0.364) ab	0.813 (0.373) a
0.5 – 1.0	0.545 (0.352) a	0.332 (0.172) a	0.420 (0.167) b	0.545 (0.232) a
1.0 – 2.0	0.347 (9.256) a	0.571 (0.166) a	0.164 (0.082) bc	0.556 (0.000) a
		20 – 40 cm		
0.01 – 0.1	0.439 (0.363) a		0.100 (0.046) a	0.719 (0.318) a
0.1 – 0.2	0.628 (0.469) a	0.588 (0.383) a	0.181 (0.099) a	0.524 (0.273) a
0.2 – 0.3	0.561 (0.359) a	0.444 (0.293) a	0.180 (0.119) a	1.01 (0.709) a
0.3 – 0.5	0.380 (0.267) a	0.298 (0.144) a	0.143 (0.121) a	0.714 (0.208) a
0.5 – 1.0	0.214 (0.074) a	0.628 (0.055) a	0.105 (0.104) a	
1.0 – 2.0	0.140 (4.628) a			0.589 (0.168) a
		0 – 40 cm		
0.01 – 0.1	0.482 (0.207) a	0.384 (0.120) b	0.748 (0.189) a	0.848 (0.243) a
0.1 – 0.2	0.742 (0.568) a	0.646 (0.144) ab	0.942 (0.526) a	1.03 (0.511) a
0.2 – 0.3	0.632 (0.417) a	0.735 (0.116)a	0.939 (0.414) a	0.949 (0.500) a
0.3 – 0.5	0.451 (0.294) a	0.645 (0.111) ab	0.919 (0.554) a	0.853 (0.454) a
0.5 – 1.0	0.420 (0.216) a	0.449 (0.124) ab	0.535 (0.351)ab	0.581 (0.293) a
1.0 – 2.0	0.250 (0.042) a	0.415 (0.300) b	0.190 (0.230)b	0.549 (0.005) a

† For each depth range, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using simple one-way ANOVA. Differences were tested using Dunnett's T3 post-hoc test for unequal variances.

‡ Differences in fine root longevity values between diameter classes at OA were tested using the REGWQ post-hoc test for equal variances.

Table 4.8: Paired-means t-tests comparing mean fine root turnover estimates from minirhizotron data for depths of 0 – 20 cm and 20 – 40 cm at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 combined. Results were not reported for diameter classes that did not have roots present at both depths. Positive *t* values mean that FR turnover values for 0 – 20 cm depth intervals are greater while negative *t* values mean that turnover values for 20 – 40 cm depth intervals are greater

Site	Diameter Class	Mean Difference	df	*t*	Sig. (2-tailed)
HJP94	0.01 − 0.1	0.144	3	3.35	0.044*
	0.1 – 0.2	0.149	3	1.42	0.250
	0.2 – 0.3	0.114	3	2.42	0.094*
	0.3 – 0.5	0.112	3	2.05	0.133
	0.5 – 1.0	0.100	3	3.96	0.029*
	1.0 – 2.0	0.053	3	1.84	0.163
OJP	0.01 − 0.1	0.260	3	0.881	0.471
	0.1 – 0.2	-0.068	3	-0.591	0.660
	0.2 – 0.3	0.012	3	0.079	0.944
	0.3 – 0.5	0.357	3	31.9	0.001*
	0.5 – 1.0	0.097	3	1.66	0.346
	1.0 – 2.0	0.042	3	0.211	0.853
OA	0.01 − 0.1	1.11	3	8.81	0.003*
	0.1 – 0.2	0.744	3	22.4	0.002*
	0.2 – 0.3	0.834	3	3.61	0.069*
	0.3 – 0.5	0.505	3	20.9	0.000*
	0.5 – 1.0	0.446	3	7.24	0.019*
	1.0 – 2.0	0.323	3	4.41	0.048*
OBS	0.01 − 0.1	0.405	3	1.21	0.314
	0.1 – 0.2	0.402	3	1.35	0.309
	0.2 – 0.3	-0.237	3	-10.7	0.009*
	0.3 – 0.5	0.152	3	6.71	0.007*
	0.5 – 1.0	0.077	3	0.800	0.508
	1.0 – 2.0	-0.094	3	-0.614	0.602

* denotes significance at $\alpha = 0.1$

4.4 Discussion

4.4.1 Root diameter class distribution

In this study, over 94% of the roots measured using MR were found to be less than 0.5 mm in diameter. At all four research sites, median diameters of the roots analyzed were found to be less than 0.3 mm; much less than the general 2 mm FR definition. Similar findings were reported by Pregitzer et al. (2002) in a study of nine North American tree species (*Acer saccharum, Liriodendron tulipifera, Populus balsamifera, Quercus alba, Picea glauca, Pinus edulis, Pinus ellioti, Pinus resinosa,* and *Juniperus monosperma*) where 75% of all root length from excavations was attributed to roots < 0.5 mm in diameter. For sugar maple and balsam poplar, all measured roots were < 0.3 mm in diameter. In another study of excavated *Acer saccharum* roots by Pregitzer et al. (1998), they found that 80% of roots analyzed were < 0.5 mm in diameter. Baddely and Watson (2005) reported in a MR study of *Prunus avium* (wild cherry) that 89% of roots had a diameter less than 0.5 mm and that approximately 68% of roots studied were less than 0.3 mm in diameter. In a study of root survivorship in apple also using MR, Wells and Eissenstat (2001) found that between 64.5 and 69.3% of roots analyzed fell within a diameter range between 0.1 and 0.3 mm.

Based on the FR diameter results of this study and the findings of other researchers, it appears that the use of the traditional diameter class definition of < 2 mm is perhaps an antiquated notion and is not representative of the roots being observed. As large populations of roots with diameters < 0.5 mm have been documented directly from root excavations, there is little concern that the small root sizes measured in this MR study among others are merely artifacts of MR data collection and analysis. It could be argued that the standard definition of a FR being ≤ 2.0 mm and a coarse root > 2 mm needs to be rethought and perhaps the use of diameter classes based on root function, nutrient content, or branching order, rather than relying on arbitrary diameters, be implemented. Further, an intermediate root class could be used to bridge the gap between fine and coarse roots. The prime concern in any study that groups things together in classes is that it is assumed that all individuals within those classes behave in a similar manner to one another. According to several root studies (Tierney and Fahey, 2001; Wells and Eissenstat, 2001), this may not be the case.

4.4.2 Fine root biomass and production with root diameter and soil depth

Fine root biomass estimates in this study were found to vary between diameter classes with biomass increasing with an increase in root diameter. However, significant differences were only found for a depth interval of 0 – 40 cm at all sites and at OA for 20 – 40 cm. Differences in biomass at all sites for a sampling depth of 0 – 40 cm is due to the larger combined biomass values of the 0 – 20 and 20 – 40 cm depths which result in a much larger range of values than the smaller depths. Although much fewer in number, roots in the larger diameter classes (> 0.5 mm) constituted the greatest amount of biomass. Several root diameter classes were found to be significantly different between the two soil depths (Table 4.3). Kummerow et al. (1990) reported that about 50% of scrub oak (*Quercus cocifera*) FR (< 1 mm) measured were found within the upper 10 cm of the soil, while this upper portion of the profile contained 26% and 40% of small roots (1 – 5 cm) and large roots (> 5 cm), respectively. Using soil cores and a 5 cm FR diameter definition in a white oak (*Quercus alba*) stand, Joslin and Henderson (1987) found that the upper 22 cm of soil contained approximately 43% of the total root mass sampled to a 100 cm depth.

Production of FR at each of the four sites was not significantly affected by diameter in this study for any depth interval. However, significant differences were found within several diameter classes between the two soil depth intervals across the four sites (Table 4.4). In this study, FR production was generally greater in the 0 – 20 cm depth interval compared to the 20 – 40 cm interval. Fine root production was found to be influenced by soil depth at OBS where half of the diameter classes were significantly different between the two depths. This is likely due to higher nutrient levels higher in the soil profile (upper depth interval) and a water table entering the rooting zone (lower depth interval). Using MR, Pregitzer and Hendrick (1996) reported that approximately 44.2% of total root length production in two Michigan hardwood forests occurred in the upper 20 of the soil profile while only 23.2% of production occurred for a depth interval of 20 – 40 cm.

While not as pronounced as expected, this study has shown that there are differences in the way that FR of different diameters can vary both in biomass and production with depth. It would also seem that due to high levels of variability, detecting differences in FR biomass and production can be difficult in small depth intervals. Intuitively, one would strive to adequately sample in smaller intervals in hopes of getting a higher resolution dataset or to capture potential influences of soil

horizonation on FR growth parameters, but doing so may make detecting small differences nearly impossible.

4.4.3 Fine root turnover and longevity with root diameter and soil depth

Fine root turnover was found to increase with a decrease in root diameter and decrease with an increase in depth (Tables 4.7 and 4.8). Many other studies reported in the literature have also reported similar patterns relating to root diameter (Gill et al., 2002; Joslin et al., 2006; Majdi et al., 2001; Pregitzer, 1998; Wells and Eissenstat, 2001) and soil depth (Burton et al., 2000; Fukuzawa et al., 2007; Hendrick and Pregitzer, 1996; Satomura et al., 2006). Joslin and Henderson (1987) found that FR < 1 mm in diameter accounted for approximately 54% of turnover, while constituting 38% of the total root mass to a 100 cm depth. Baddeley and Watson (2005) noted that root survival decreased with root diameter and soil depth, however, Gill et al. (2002) found that there were no significant differences in turnover within the soil profile. Turnover values in the shortgrass steppe of Colorado, USA, as reported by Gill et al. (2002), were approximately 0.83 and 0.89 yr^{-1} for depth intervals of 0 – 20 and 20 – 40, respectively. In a study of a northern hardwood forest dominated by sugar maple (*Acer saccharum*), American Beech (*Fagus grandifolia*), yellow birch (*Betula alleghamiensis*), and red maple (*Acer rubrum*), Burke and Raynal (1994) reported turnover values ranging from 0.7 to 2.0 yr^{-1}. Ruess et al. (1996) in a study of taiga forests in Alaska reported FR turnover values of 1.05, 0.33 and 0.52 yr^{-1} for black spruce, birch-aspen, and white spruce stands, respectively. Using three of the same sites as in this study, Steele et al. (1997) reported turnover values of approximately 1.6, 1.7 , and 2.9 yr^{-1} for OJP, OA, and OBS, respectively. These results were obtained using a ratio of FR mortality to initial FR length as described by Hendrick and Pregitzer (1992b). The values reported by Steele et al. (1997) are much greater than those reported for boreal forest species in the literature. Steele et al. (1997) suggested that differences in climate between the BERMS locations and those of other researchers could be partially responsible for the higher turnover rates; however, our values, which are much lower, were obtained from the same sites. The theory that turnover is greater in warmer climates compared to cooler ones has been proposed by several authors, but is still poorly understood (Eissenstat et al., 2000b; Gill and Jackson, 2000; Hendrick and Pregitzer, 1993; Watson et al., 2000). Other authors suggest that this may not be the case and that FR turnover in northern sites are comparable to those of more temperate locations (Ruess et al., 1996; Ruess et al., 2005; Ruess et al., 2003).

Longevity values were found to increase with an increase in root diameter, a general trend found by other authors as well (Tierney and Fahey, 2001; Wells and Eissenstat, 2001). Values reported in this study for FR longevity (Table 4.5) are higher than those reported in some of the literature. In this study, all estimates of root longevity were greater than one year. In a study of apple tree roots in South Carolina, Wells and Eissenstat (2001) found that FR were very short-lived with lifespans of only 36 to 114 days (0.10 to 0.3 years). In 1999, as referenced in Eissenstat et al. (2000b), Wells reported lifespans of less than 300 days (0.82 years) for sugar maple roots < 0.25 mm in diameter and more than 600 days (1.64 years) for roots > 0.25 mm in diameter. For a New Hampshire hardwood forest, Tierney and Fahey (2001) estimated a range of root lifespans from 138 to 494 days (0.38 to 1.35 years). Due to the method used to calculate longevity in this study, large longevity values, particularly at the OA site, result from large mean annual root biomass values and low production values. The use of cohort analysis may have resulted in a more accurate estimation of FR longevity in this study (Block, 2004). However, due to data constraints regarding the minimum number of roots required within a given cohort (Hooker et al., 2000), cohort analysis was not used.

While root diameter and soil depth have been named as two of the most critical factors, there are many other factors that are also believed to have influence on patterns of FR turnover rates and longevity. Soil environmental factors such as temperature, moisture, and fertility can vary greatly with depth and are believed to contribute to turnover rates for a given species or location (Bloomfield et al., 1996; Gill and Jackson, 2000; Santantonio and Grace, 1987; Satomura et al., 2007). Soil horizonation can also play a role in FR distribution (Sainju and Good, 1993). Tree roots tend to proliferate in nutrient rich surface horizons, while more nutrient poor and potentially water-logged horizons at depth tend to have fewer roots. Competition between roots has also been identified as a factor controlling FR survival. On the one hand, small roots are more likely to have a "near-neighbor" competing for the same resources, leading to an increase in the risk of mortality. On the other hand, larger, more mature roots generally had fewer neighbors and a lower hazard value (instantaneous risk of mortality at a given time) (Wells and Eissenstat, 2001; Wells and Eissenstat, 2003; Wells et al., 2002). It has been suggested that root age can affect the survivorship of a root, with older roots having a better chance of survival. Individual root ages were not measured in this study; however, a study that employed the use of cohort analysis could make these comparisons. Using cohort analysis, Wells and Eissenstat (2001) compared the longevity between roots of varying

pigmentation and found that older brown roots had a slightly longer lifespan. Similarly, root order also influences root survivorship with higher order roots being less likely to die (Guo et al., 2007; Hishi, 2007; Majdi et al., 2001; Pregitzer et al., 1997). The infection of roots by mycorrhizae has been found to greatly increase FR longevity as compared to non-infected roots (King et al., 2002). However, in a study of *Populus generosa inter Americana*, Hooker (1995) found that mycorrhizal colonization of roots led to a reduction in FR longevity. With so many contributing factors, the study of the mechanisms behind FR turnover and longevity requires much more attention in future studies.

4.5 Conclusion

The conventional definition of a FR having a diameter less < 2 mm may not be sufficient to capture subtle differences in FR dynamics. The vast majority of roots at each of the four research sites in this study (85, 90, 96, and 96% at HJP94, OJP, OA, and OBS, respectively), were < 0.5 mm in diameter. Differences in FR biomass, turnover, and longevity were detected between some, but not all, diameter classes. This reaffirms that even at a scale of one-tenth of a millimeter, there are physiological differences such as root longevity and rates of production between roots of different diameters. Significant differences in the FR parameters mentioned previously were also found between the various soil depths investigated in this study between depths and between diameter classes at each depth. A general trend of increasing FR longevity and decreasing turnover was noted with an increase in soil depth as well as root diameter.

Future studies should take into account the heterogeneities found between roots less than 0.5 mm in diameter both in this study and in others. The use of more functionally based diameter class definitions such as root order, tissue density, or nutrient content has the potential to provide greater insight into the dynamic processes that are occurring within the soil. By moving toward the use of functional diameter classes in FR studies, we stand to increase the accuracy in which we are able to detect differences in FR parameters such as production and longevity. This increased accuracy in estimating belowground FR trends will, in turn, serve to increase the accuracy of global C models and their ability to better predict the effects of global climate change.

4.6 Literature Cited

Baddeley, J., and C. Watson. 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant Soil 276:15-22.

Bernier, P.Y., and G. Robitaille. 2004. A plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265:165-173.

Block, R.M.A. 2004. Fine root dynamics and carbon sequestration in juvenile hybrid poplar plantations in Saskatchewan, Canada, University of Saskatchewan, Saskatoon, SK.

Bloomfield, J., K. Vogt, and P.M. Wargo. 1996. Tree turnover and senescence, p. 363-381, *In* Y. Waisel, et al., eds. Plant Roots: the hidden half., 2nd ed. Marcel Dekker, New York.

Brunner, I., and D.L. Godbold. 2007. Tree roots in a changing world. J. For. Res. 12:78-82.

Burke, M.K., and D.J. Raynal. 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135-146.

Burton, A.J., K.S. Pregitzer, and R.L. Hendrick. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia 125:389-399.

Chen, X., D. Eamus, and L.B. Hutley. 2004. Seasonal patterns of fine-root productivity and turnover in a tropical savanna of northern Australia. J. Trop. Ecol. 20:221-224.

Eissenstat, D.M., C.E. Wells, R.D. Yanai, and J.L. Whitbeck. 2000a. Research view: building roots in a changing environment: implications for root longevity. New Phytol. 147:33-42.

Eissenstat, D.M., C.E. Wells, R.D. Yanai, and J.L. Whitbeck. 2000b. Building roots in a changing environment: implications for root longevity. New Phytol. 147:33-42.

Field, A. 2005. Discovering Statistics Using SPSS. 2nd ed. Sage Publications Ltd., London, England.

Fukuzawa, K., H. Shibata, K. Takagi, F. Satoh, T. Koike, and K. Sasa. 2007. Vertical distribution and seasonal pattern of fine-root dynamics in a cool–temperate forest in northern Japan: implication of the understory vegetation, Sasa dwarf bamboo. Ecol. Res. 22:485-495.

Gill, R.A., I.C. Burke, W.K. Lauenroth, and D.G. Milchunas. 2002. Longevity and turnover of roots in the shortgrass steppe: influence of diameter and depth. Plant Ecol. 159:241-251.

Gill, R.A., and R.B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147:13-31.

Guo, D., H. Li, R.J. Mitchell, W. Han, J.J. Hendricks, T.J. Fahey, and R.L. Hendrick. 2007. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. New Phytol. 0:1-14.

Hendrick, R.L., and K.S. Pregitzer. 1992a. Spatial variation in tree root distribution and growth associated with minirhizotrons. Plant Soil 143:283-288.

Hendrick, R.L., and K.S. Pregitzer. 1992b. The demography of fine roots in a northern hardwood forest. Ecology 73:1094-1104.

Hendrick, R.L., and K.S. Pregitzer. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Can. J. For. Res. 23:2507-2520.

Hendrick, R.L., and K.S. Pregitzer. 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. J. Ecol 84:167-176.

Hishi, T. 2007. Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. J. For. Res. 12:126-133.

Hooker, J.E., R. Hendrick, and D. Atkinson. 2000. The measurement and analysis of fine root longevity, p. 273-304, *In* A. L. Smit, et al., eds. Root Methods: A Handbook. Springer, New York.

Hooker, J.E., K.E. Black, R.L. Perry, and D. Atkinson. 1995. Arbuscular mycorrhizal fungi induced alteration to root longevity of poplar. Plant Soil 172:327-329.

Jackson, R.B., J. Canadell, J.R. Ehleringer, H.A. Mooney, O.E. Sala, and E.D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411.

Joslin, J.D., and G.S. Henderson. 1987. Organic matter and nutrients associated with fine root turnover in a white oak stand. For. Sci. 33:330-346.

Joslin, J.D., J.B. Gaudinski, M.S. Torn, W.J. Riley, and P.J. Hanson. 2006. Fine-root turnover patterns and their relationship to root diameter and soil depth in a ^{14}C-labeled hardwood forest. New Phytol. 172:523-535.

Kalyn, A. 2005. Fine root dynamics and belowground carbon-cycling in the boreal forests of Saskatchewan., University of Saskatchewan, Saskatoon, SK, Canada.

King, J.S., T.J. Albaugh, H.L. Allen, M. Buford, B.R. Strain, and P. Dougherty. 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154:389-398.

Kummerow, J., M. Kummerow, and L. Trabaud. 1990. Root biomass, root distribution and the fine-root growth dynamics of *Quercus coccifera* L. in the garrigue of southern France. Plant Ecol. 87:37-44.

Majdi, H., and P. Andersson. 2005. Fine root production and turnover in a Norway spruce stand in northern Sweden: effects of nitrogen and water manipulation. Ecosystems 8:191-199.

Majdi, H., E. Damm, and J.-E. Nylund. 2001. Longevity of mycorrhizal roots depends on branching order and nutrient availability. New Phytol. 150:195-202.

Majdi, H., K. Pregitzer, A.-S. Morén, J.-E. Nylund, and G. I. Ågren. 2005. Measuring fine root turnover in forest ecosystems. Plant Soil 276:1-8.

Ostonen, I., K. Lõhmus, and K. Pajuste. 2005. Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. For. Ecol. Manag. 212:264-277.

Pregitzer, K.S., M.E. Kubiske, C.K. Yu, and R.L. Hendrick. 1997. Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia 111:302-308.

Pregitzer, K.S., J.L. DeForest, A.J. Burton, M.F. Allen, R.W. Ruess, and R.L. Hendrick. 2002. Fine root architecture of nine North American trees. Ecol. Monogr. 72:293-309.

Pregitzer, K.S., Laskowski, M. J., Burton, A. J., Lessard, V. C., Zak, D. R. 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol. 18:665-670.

Ruess, R.W., K. Van Cleve, J. Yarie, and L.A. Vierek. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can. J. For. Res. 26:1326-1336.

Ruess, R.W., R.L. Hendrick, J.G. Vogel, and B. Sveinbjornsson. 2005. The role of fine roots in the functioning of Boreal forests, pg 189-210, *In* F. S. Chapin III, et al., eds. Alaska's changing boreal forest. Oxford University Press, New York, NY.

Ruess, R.W., R.L. Hendrick, A.J. Burton, K.S. Pregitzer, B. Sveinbjornsson, A. M.F., and G.E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol. Monogr. 73:643-662.

Sainju, U.M., and R.E. Good. 1993. Vertical root distribution in relation to soil properties in New Jersey Pinelands forests. Plant Soil 150:87-97.

Santantonio, D., and J.C. Grace. 1987. Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Can. J. For. Res. 17:900-908.

Satomura, T., K. Fukuzawa, and T. Horikoshi. 2007. Considerations in the study of tree fine-root turnover with minirhizotrons. Plant Root 1:34-45.

Satomura, T., Y. Hashimoto, H. Koizumi, K. Nakane, and T. Horikoshi. 2006. Seasonal patterns of fine root demography in a cool-temperate deciduous forest in central Japan. Ecol. Res. 21:741-753.

Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17:577-587.

Tierney, G.L., and T.J. Fahey. 2001. Evaluating minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest. Plant Soil 229:167-176.

Watson, C.A., J.M. Ross, U. Bagnaresi, G.F. Minotta, F. Roffi, D. Atkinson, K.E. Black, and J.E. Hooker. 2000. Environment-induced modifications to root longevity in *Lolium perenne* and *Trifolium repens*. Ann. Bot. 85:397-401.

Wells, C.E., and D.M. Eissenstat. 2001. Marked differences in survivorship among apple roots of different diameters. Ecology 82:882-892.

Wells, C.E., and D.M. Eissenstat. 2003. Beyond the roots of young seedlings: the influence of age and order on fine root physiology. J. Plant Growth Regul. 21:324-334.

Wells, C.E., D.M. Glenn, and D.M. Eissenstat. 2002. Changes in the risk of fine-root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). Am. J. Bot. 89:79-87.

5 IMPACT OF MINIRHIZOTRON TUBES ON FINE ROOT DISTRIBUTION IN THE BOREAL FOREST OF SASKATCHEWAN

5.1 Introduction

As forest research begins to shift its focus from well understood aboveground components to the lesser known below ground fraction which are more difficult to study, new and exciting techniques are being employed by researchers. One of the most notable innovations in the study of fine roots (FR, roots < 2 mm in diameter), is the minirhizotron (MR) (Hendrick and Pregitzer, 1996; Johnson et al., 2001; Satomura et al., 2007). Minirhizotron systems generally consist of clear cellulose acetate butyrate tubes (among other materials) 65.5 mm in diameter and up to 2 m long inserted into the ground at an angle ranging from 30 to 45º from horizontal (Ephrath et al., 1999; Hendricks et al., 2006; Withington et al., 2003). As roots intersect the surface of the MR tubes, images are collected using a modified video camera and analyzed to calculate a number of FR parameters such as biomass, production, longevity, and turnover. One of the primary assumptions of the MR technique is that roots growing along the surface of the MR tube are representative of those in the bulk soil (Hendricks et al., 2006).

A large number of studies have been conducted to estimate the potential effects of MR tube installation and subsequent sampling on estimates of FR growth parameters. One of the main issues discussed in the literature is the proliferation of FR from root segments damaged during tube installation (Burke and Raynal, 1994; Hendrick and Pregitzer, 1996; Joslin and Wolfe, 1999; Majdi, 1996). This sudden burst of root growth can result in a large overestimation of FR biomass and production in the first year or so after tube installation. As such, most studies do not commence image collection for a year following tube installation, allowing for the tubes to equilibrate or return to a state that better represents the bulk soil. The installation process can also result in a flush of nitrogen being released from the soil which can also result in increased root production (Joslin and Wolfe, 1999; Pregitzer et al., 1993). Other factors studied that could potentially affect root growth at the soil/tube interface include installation angle (Bohm et al., 1977; Ephrath et al., 1999; Johnson et al., 2001; Van Noordwijk et al., 1985), gaps and voids in the soil (Gijsman et al., 1991; Phillips et al., 2000; Van Noordwijk et al., 1985; Volkmar, 1993), changes in soil bulk density surrounding the MR tubes (Volkmar, 1993), MR tube

material (Withington et al., 2003), and possible changes in soil temperature from MR camera lights (Van Rees, 1998).

A review of pertinent literature did not reveal any studies that had specifically looked at FR parameters measured at different orientations around the MR tube (above, sides, and below). Most MR studies collect root images along the top of the tube. Duback and Russelle (1995) compared FR production and turnover in alfalfa (*Medicago sativa*) and birdsfoot trefoil (*Lotus corniculatus*) between the sides of horizontally installed MR tubes. They did not collect MR data from the top of the MR tubes partially due to the accumulation of water droplets that they felt may affect root growth, branching patterns, and root senescence. There are several studies documenting MR tube excavations (Bohm et al., 1977; Johnson et al., 2001; Phillips et al., 2000), but few discuss details on what was observed in these excavations, particularly in regard to root location and orientation around or along the tubes.

The objectives of this study, therefore, were to 1) determine the effect of image location (top and sides) in MR tubes on FR biomass and production at three boreal sites in Saskatchewan, and 2) excavate several MR tubes to gain a better understanding of how roots behave when they come in contact with an obstruction such as a MR tube and how a potential change in rooting path could possibly affect MR estimates of FR growth parameters.

5.2 Materials and methods

5.2.1 Site Descriptions

The three sites used in this study include a young jack pine stand (HJP94) and mature jack pine (OJP) and aspen (OA) stands located in the boreal forest of northern Saskatchewan, Canada. The sites are part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) study north of Prince Albert, SK. More detail on each of these sites can be found in Section 3.2.1 and Table 3.1 in Chapter 3 of this thesis.

5.2.2 Minirhizotron data collection and processing

Digital images were collected monthly from three MR tubes at the HJP94, OJP, and OA sites from June to August in 2006. Minirhizotron images were collected along the top, left, and right sides of the tubes. The MR tubes were installed during the summer of 2002 and were arranged in three banks of four tubes in a nested design, with each bank representing an individual nest (Hendrick and Pregitzer, 1992). Only the fourth tube from each bank was used in this study (data from the

other nine tubes are presented in Chapter 3). Minirhizotron images for all tubes at each of the sites were truncated at a vertical depth of 40 cm (54 images) as this is the maximum depth attained by the shallowest tube at OA.

Image analysis was performed using RooTracker root analysis software (Version 2.0.3b1, Duke University, NC, USA). Fine root biomass and production values were calculated from the RooTracker output data using the plane intersect method proposed by Bernier and Robitaille (2004) in SAS (Version 9.1, SAS Institute Inc, Cary, NC, USA). A more detailed description of the MR system and image and data analysis can be found in Section 3.2.2 in Chapter 3 of this thesis.

5.2.3 Minirhizotron tube excavation

Minirhizotron tubes were excavated at HJP94, OJP, and OA to visually assess the rooting paths directly adjacent to the tubes. Two of the three tubes at each site that were used for the image location study were selected for excavation. Actual selection of the tubes was done in the field based on possible ease of extraction and minimization of damage to surrounding trees.

For each excavation, a rectangular access pit was dug alongside the MR tube that was 50 x 150 cm and 75 – 100 cm deep with a 5 – 10 cm buffer away from the tube (Plate 5.1). This buffer area was maintained to minimize disturbance to any roots that needed to be cut during the excavation. The MR tubes were carefully excavated along the top and one side using a variety of tools including spoons, paint brushes, picks, and scoops. Removing soil from only the top and side of the tube minimized the chance of disturbing the roots growing along and around the tube and provided an opportunity to view intact and undisturbed roots in the soil adjacent to the tube by looking through the uncovered side of the tube. A visual assessment of rooting paths was made prior to the removal of the tubes from the ground.

5.2.4 Statistical analysis

Statistical analyses in this study were completed using a combination of SAS and SPSS (SPSS for Windows, Release 14.0.0, SPSS Inc, Chicago, IL, USA) statistical software packages. Initial application of the plane intersect method (PIM) to the raw MR data from RooTracker was done using SAS (Bernier and Robitaille, 2004). Data output from the PIM were then statistically analyzed in SPSS. Differences in FR biomass and production between image orientations were tested using Ryan-Einot-Gabriel-Welsch *Q* (REGWQ) in a one-way ANOVA ($\alpha = 0.10$). The REGWQ test maintains tight control of Type I error while maintaining good

statistical power (Field, 2005). Values for FR biomass and production were transformed to fit a normal distribution using square root and natural log transformations, respectively, and verified using the Kolmogorov-Smirnov goodness-of-fit test.

5.3 Results

5.3.1 Fine root biomass and production

Fine root biomass ranged from 3.91 to 6.48, 1.16 to 2.88, and 1.68 to 4.60 Mg ha^{-1} for all three image orientations at HJP94, OJP, and OA, respectively. There were no significant differences in FR biomass found among any of the three image orientations at all sites (Table 5.1, Figure 5.1). Fine root production for the top orientation was found to be significantly higher than the sides for July at OA (Table 5.1, Figure 5.2). No significant differences in FR production were found at HJP94 or OJP. A summary of the one-way ANOVAs done in this study can be found in Appendix E, Table E.1. No general patterns of FR biomass or production were noted among any of the three image orientations. Fine root biomass and production increased for all orientations from July to August at all sites.

5.3.2 Minirhizotron tube excavation

Excavation of the MR tubes yielded several interesting observations. Many roots were found to be growing downward along the length of the tubes on the tops, sides, and bottoms rather than around them (Plate 5.2). This rooting pattern was most predominant at the sandy jack pine sites although it was also witnessed at the OA site as well. Large root masses were also observed growing on the underside along the length of the MR tubes (Plate 5.3). The vertical depths at which roots were found beneath the tubes ranged from 2 cm at OA to > 90 cm at HJP94. One single root at HJP94 was found to have grown 104 cm along the bottom of the MR tube. Most roots unearthed surrounding the MR tubes at HJP94 and OA were less than 2 mm in diameter. At OJP, few roots were found in the soil profile and many of those found to a vertical depth of 20 cm were greater than 2 mm in diameter. Each of the tubes that were excavated at OA were found to have a substantial amount of surface organic matter pulled down into the MR hole along the bottom side of the MR tubes during tube installation (Plate 5.4).

Table 5.1: Mean fine root biomass and production estimates from minirhizotron data for young jack pine (HJP94), mature jack pine (OJP), and mature aspen (OA) stands in the boreal forest of northern Saskatchewan in July and August of 2006. Values in parentheses represent 1 SD (N=3).

Month	Sample orientation	Site		
		HJP94	OJP	OA
		Mean fine root biomass		
		---------- Mg ha^{-1} ----------		
July	Left	4.61 (0.054) a†	1.16 (0.302) a	1.83 (0.089) a
	Top	3.91 (0.297) a	2.15 (0.365) a	4.30 (0.507) a
	Right	6.01 (1.39) a	2.66 (0.078) a	1.68 (0.198) a
August	Left	4.85 (0.055) a	1.28 (0.261) a	2.16 (0.052) a
	Top	4.25 (0.270) a	2.47 (0.363) a	4.60 (0.608) a
	Right	6.48 (1.43) a	2.88 (0.132) a	2.24 (0.296) a
		Mean fine root production		
		---------- Mg ha^{-1} mo^{-1} ----------		
July	Left	0.704 (0.708) a†	0.376 (0.072) a	0.559 (0.032) a
	Top	0.507 (0.112) a	0.462 (0.166) a	1.75 (0.036) b
	Right	0.894 (0.359) a	0.759 (0.024) a	0.686 (0.054) a
August	Left	0.265 (0.011) a	0.171 (0.020) a	0.364 (0.012) a
	Top	0.500 (0.000) a	0.351 (0.020) a	0.449 (0.057) a
	Right	0.583 (0.065) a	0.613 (0.334) a	0.649 (0.266) a

† For each month, means followed by the same letter in a column are not significantly different ($\alpha = 0.10$) using simple one-way ANOVA.

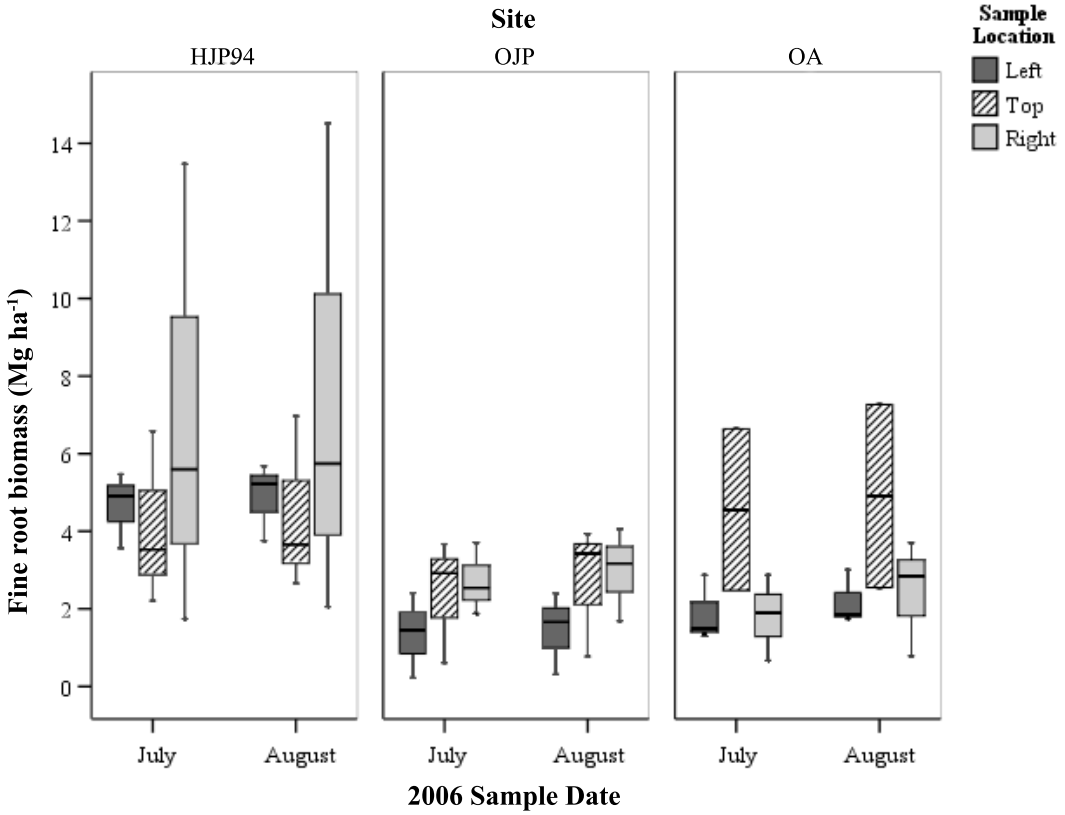

Figure 5.1: Fine root biomass estimates from minirhizotron data for young jack pine (HJP94), mature jack pine (OJP), and mature aspen (OA) stands in the Boreal forest of northern Saskatchewan in July and August of 2006. Error bars represent one standard deviation and horizontal lines within each bar represent the median FR biomass value.

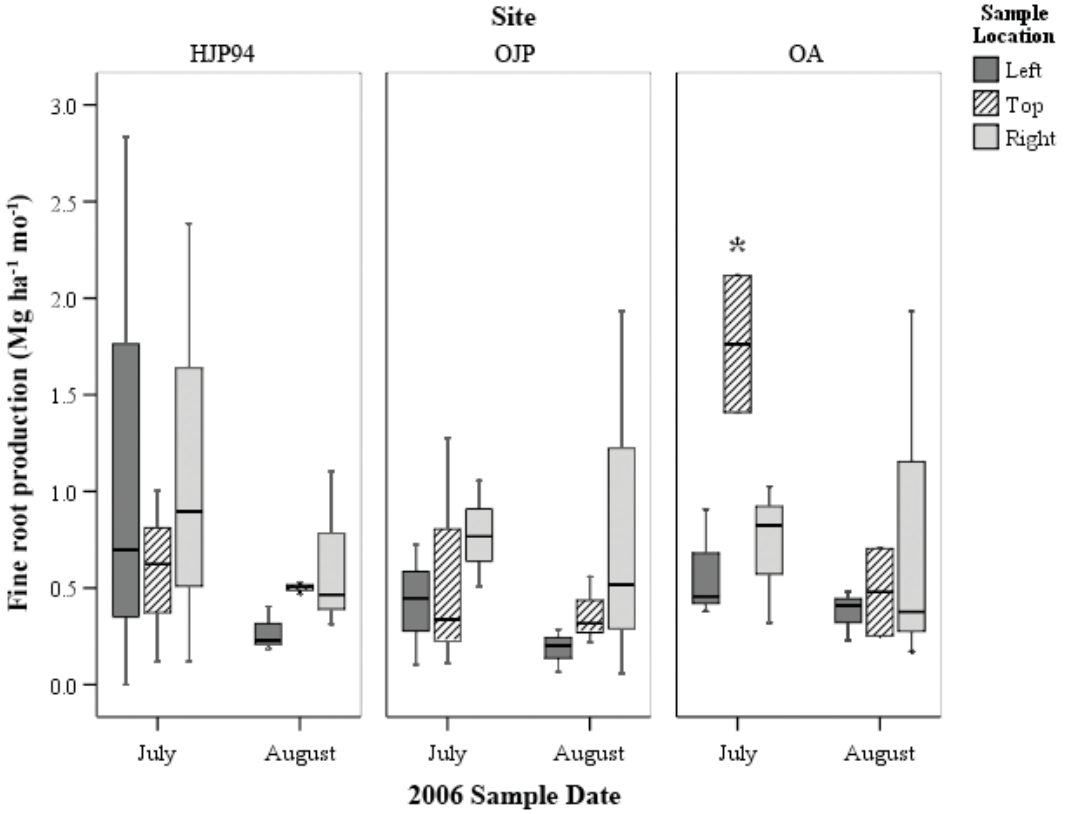

Figure 5.2: Fine root production estimates from minirhizotron data for young jack pine (HJP94), mature jack pine (OJP), and mature aspen (OA) stands in the boreal forest of northern Saskatchewan in July and August of 2006. Error bars represent one standard deviation and horizontal lines within each bar represent the median fine root biomass value. * denotes a significant difference ($\alpha = 0.10$) using simple one-way ANOVA.

Plate 5.1: Soil pit and partially exposed minirhizotron tube at the mature jack pine site (OJP). Fine roots (< 2 mm) can be seen growing around the tube.

Plate 5.2: Image showing several fine roots (< 2 mm) during excavation growing parallel with the length of a minirhizotron tube at a young jack pine site (HJP94).

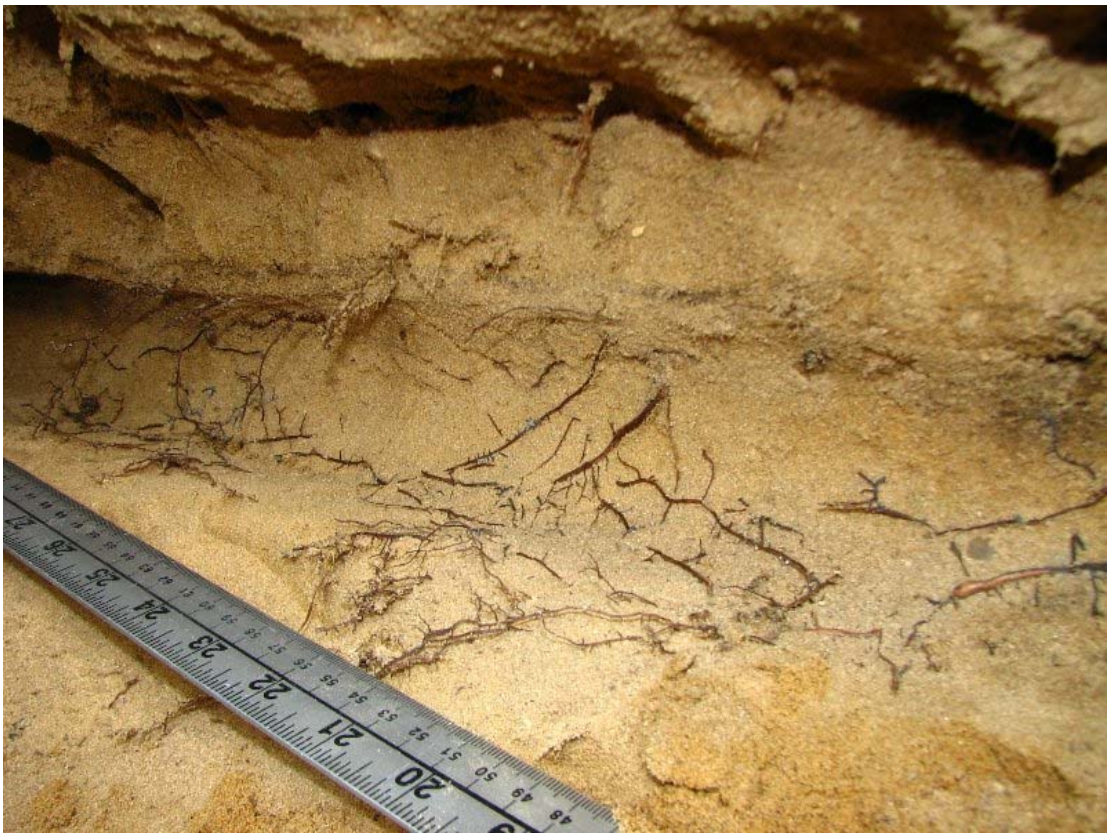

Plate 5.3: Image showing a large number of fine roots (< 2 mm) growing beneath a minirhizotron tube (after tube removal) at a young jack pine site in northern Saskatchewan.

Plate 5.4: Image depicting nutrient rich organic matter from the surface pushed into the mineral soil during minirhizotron tube installation at a mature aspen site in northern Saskatchewan.

5.4 Discussion

5.4.1 Fine root biomass and production for different sample orientations

Calculated estimates of FR biomass and production in this study were found to be similar to those reported on a full site basis at HJP94, OJP, and OA in Chapter 3 of this thesis (Tables 3.2 and 3.5). The lack of significant differences in FR biomass between the top and sides of the MR tubes in this study suggests that the standard practice of acquiring root images along the top side of the tube represents the root dynamics in the soil and should not bias the root biomass estimates. Similarly, no significant differences in FR production were detected between sample orientations for all sites with the exception of OA in July of 2006 where production along the top of the MR tube was found to be significantly greater than either side of the tube (FR biomass along the tops of the tubes was larger than that of the sides at OA, although not by a statistically significant amount). One possible reason for a greater level of FR production in July could be a flush of FR growth early in the summer which leveled off by August (McMichael and Quisenberry, 1993; McMichael and Burke, 1996). Due to the limited sampling periods in this study, it is difficult to be certain of the timing of such seasonal fluctuations in root growth. However, a sizeable spike in FR production was noted for this same period at OA in Chapter 3 (Figure 3.3 and Table 3.4), so one could infer that the July rise in production in this study was related to an early season flush in FR related to an increase in soil temperature and moisture, and aboveground foliage production. It is unclear why this rise in production along the tops of the tubes at OA was not reflected in the FR production estimates for the sides of the tubes. In their study of root production and turnover using horizontal MR tubes, Dubach and Russelle (1995) found that root counts along the tubes were highly variable both along the tubes and between the sides. They found that there was no spatial pattern in root numbers along the tubes and were unable to fit the data to a normal curve. As a result of this high variability, Dubach and Russelle pooled the data from both sides of the tubes together for the remainder of the analysis. However, in this study, the values between the sides of the tubes at OA were very similar to one another. It is possible that the heart-shaped root system of the aspen in dense clayey soils could intercept the MR tubes and deflect laterally, not continuing down the sides of the tubes. Meanwhile, jack pine tap roots in sand would perhaps be more likely to follow gravity and the contours of the tubes. The differences in root morphology and

soil type could perhaps explain the vast differences between the tops and sides of the MR tubes at OA compared to relatively even root distribution around the tubes at HJP94 and OJP.

5.4.2 Minirhizotron tube excavation

It was noted that several MR tubes had surficial organic material at depth along the tube hole, likely an artifact of tube installation. Most of the organic material was found along the bottom of the tube. One particular tube at OA was found to have surficial organic material pushed approximately 35 cm along the bottom of the tube hole. This organic matter could potentially have become a source of nutrients in a nutrient poor site, encouraging root proliferation along the MR tubes (Joslin and Wolfe, 1999).

Soil moisture condensing along the bottom of MR tubes may have an influence on the region of soil below them (Dubach and Russelle, 1995). Surface runoff could potentially follow the path of least resistance and flow along the bottom of the tube. It is also possible that as moisture percolates down through the soil and intercepts the tubes, the water then follows the curvature of the tubes to the underside. Soil temperature could have also been increased at depth by the MR tubes. A combination of increases in soil moisture and soil temperature could have a positive impact on FR growth (Vogt et al., 1998).

Installing MR tubes at an angle between 30 and 45º from the horizontal has been found to reduce the incidence of preferential rooting paths as compared to vertically oriented tubes (Ephrath et al., 1999). However, if very good contact is not maintained between the soil and the tube, then it is possible for roots to proliferate in these voids (Van Noordwijk et al., 1985). While poor soil contact is more common in clayey soils than in sandy soils, gaps and voids were witnessed at all sites during image analysis.

It is possible that a several factors such as surface organic matter being pushed into the MR hole during installation, altered soil moisture and temperature around the MR tubes, and improper soil/tube contact could have contributed to the root proliferation below the MR tubes.

5.5 Conclusion

With an increasing interest in the belowground fraction of plant production in forest studies the MR technique has gained great popularity. Minirhizotron studies are done through the analysis of root images collected along the top side of the MR

tubes. This study tested the assumption that FR growth parameters such as biomass and production were the same along the top and sides of the MR tubes. No significant differences were found in FR biomass and production at three boreal sites in northern Saskatchewan with the exception of OA in July of 2006 where production was found to be higher along the top as compared to the sides. Although the sampling times cover three months, the similarity between the three tube locations (top and either side) suggest that root growth is uniform around installed tubes and would likely represent the bulk soil.

The substantial amount of roots found growing on the underside along the length of the MR tubes during tube excavation was likely due to a combination of factors such as nutrient availability, soil moisture and temperature, and possible inconsistencies in the soil/tube interface. This abundance of roots compared to the top or sides of the tube suggests that fine root dynamics measured at the bottom of the tube may be overestimated compared to the other locations. However, in hindsight, MR data should have also been collected along the bottoms of the tubes.

Overall, it may be assumed that the traditional practice of using images collected along the top side of the MR tubes is acceptable and will result in estimates of FR biomass and production that represent the bulk soil. Future research into root proliferation below installed MR tubes is encouraged to better understand the mechanisms involved and potential solutions to minimize this phenomenon. On a similar note, more research into maximizing soil/tube contact during MR tube installation is also suggested.

5.6 Literature Cited

Bernier, P.Y., and G. Robitaille. 2004. A plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265:165-173.

Bohm, W., H. Maduakor, and H.M. Taylor. 1977. Comparison of five methods for characterizing soybean rooting density and development. Agron. J. 69:415-419.

Burke, M.K., and D.J. Raynal. 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135-146.

Ephrath, J.E., M. Silberbush, and P.R. Berliner. 1999. Calibration of minirhizotron readings against root length density data obtained from soil cores. Plant Soil 209:201-208.

Field, A. 2005. Discovering Statistics Using SPSS. 2nd ed. Sage Publications Ltd., London, England.

Gijsman, A.J., J. Floris, M. Noordwijk, and G. Brouwer. 1991. An inflatable minirhizotron system for root observations with improved soil/tube contact. Plant Soil 134:261-269.

Hendrick, R., and K. Pregitzer. 1996. Applications of minirhizotrons to understand root function in forests and other natural ecosystems. Plant Soil 185:293-304.

Hendrick, R.L., and K.S. Pregitzer. 1992. Spatial variation in tree root distribution and growth associated with minirhizotrons. Plant Soil 143:283-288.

Hendricks, J.J., R.L. Hendrick, C.A. Wilson, R.J. Mitchell, S.D. Pecot, and D. Guo. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J. Ecol. 94:40-57.

Johnson, M.G., D.T. Tingey, D.L. Phillips, and M.J. Storm. 2001. Advancing fine root research with minirhizotrons. Env. Exp. Bot. 45:263-289.

Joslin, J.D., and M.H. Wolfe. 1999. Disturbances during minirhizotron installation can affect root observation data. Soil Sci. Soc. Am. J. 63:218-221.

Majdi, H. 1996. Root sampling methods - applications and limitations of the minirhizotron technique. Plant Soil 185:255-258.

McMichael, B.L., and J.E. Quisenberry. 1993. The impact of the soil environment on the growth of root systems. Env. Exp. Bot. 33:53-61.

McMichael, B.L., and J.J. Burke. 1996. Temperature effects on root growth, p. 383−396 Plant roots: the hidden half, 2nd ed. Marcel Dekker, Inc., New York, NY, USA.

Phillips, D.L., M.G. Johnson, D.T. Tingey, C. Biggart, R.S. Nowak, and J.C. Newsom. 2000. Minirhizotron installation in sandy, rocky soils with minimal soil disturbance. Soil Sci. Soc. Am. J. 64:761-764.

Pregitzer, K.S., R.L. Hendrick, and R. Fogel. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytol. 125:575-580.

Satomura, T., K. Fukuzawa, and T. Horikoshi. 2007. Considerations in the study of tree fine-root turnover with minirhizotrons. Plant Root 1:34-45.

Soil Classification Working Group. 1998. The Canadian System of Soil Classification. 3rd ed. Agric. and Agri-Food Can. Publ. 1646 (Revised). NRC Research Press, Ottawa, ON, Canada.

Van Noordwijk, M., A. Jager, and J. Floris. 1985. A new dimension to observations in minirhizotrons: A stereoscopic view on root photographs. Plant Soil 86:447-453.

Van Rees, K.C.J. 1998. Soil temperature effects from minirhizotron lighting systems. Plant Soil 200:113-118.

Vogt, K.A., D.J. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 200:71-89.

Volkmar, K.M. 1993. A comparison of minirhizotron techniques for estimating root length density in soils of different bulk densities. Plant Soil 157:239-245.

Withington, J.M., A.D. Elkin, B. Bulaj, J. Olesinski, K.N. Tracy, T.J. Bouma, J. Oleksyn, L.J. Anderson, J. Modrzynski, P.B. Reich, and D.M. Eissenstat. 2003. The impact of material used for minirhizotron tubes for root research. New Phytol. 160:533-544.

6 GENERAL DISCUSSION AND SUMMARY

With anthropogenic carbon dioxide (CO_2) emissions continuing to increase and climate change becoming a global concern, researchers have been trying to gain a better understanding of the global carbon (C) budget. As such, potential terrestrial C sinks such as the boreal forest have garnered particular interest over the course of the past decade or so. In the boreal forest, approximately 13% of total ecosystem C is sequestered in biomass with 89% of that in the belowground component (Malhi et al., 1999). The role of fine roots (FR) in boreal C-cycling is still poorly understood but with the advent of the minirhizotron (MR) system researchers are better equipped to measure FR dynamics.

In cooperation with Fluxnet Canada Research Network (FCRN), this project employed the use of MR to garner a better understanding of how FR cycle at four sites in the boreal forest of northern Saskatchewan. Over the course of four years, FR biomass continued to increase slightly, indicating that FR production was greater than FR mortality. Significant intra-annual variability in FR production was found at each of the four sites, peaking in early to midsummer and declining into the fall. No significant differences were found between MR estimates of FR biomass and those measured from soil cores. As soil cores are often considered the standard in many root studies for root biomass, having similar biomass results from MR in this study helps to validate the use of the plane intersect method in the conversion of raw MR data to biomass (although the data presented only represents one month).

At all four sites, the vast majority of ecosystem biomass C was found to be located in the stems, forest floor, and mineral soil, with little contribution from FR. However, FR C production was found to be a very important part of total net primary production (NPP), particularly at HJP94 and OBS where FR C production accounted for approximately half of the total ecosystem C production. The deciduous aspen site had a lower ratio of belowground C NPP to total C NPP as compared to the three coniferous sites, perhaps due to increased soil fertility. With FR being such a large contributing factor to total NPP, it becomes apparent that being able to accurately model FR dynamics is crucial to completing a C budget for the boreal forest.

Soil depth was found to influence FR biomass, longevity, and turnover. Fine root longevity generally increases with soil depth and root diameter while turnover decreased. The vast majority (85 – 96%) of FR measured in this study were found to be less than 0.5 mm in diameter. Significant differences in FR biomass, turnover, and

longevity were found between some, but not all, diameter classes. These differences between roots of different diameter classes challenge the traditional practice of assigning FR to an arbitrary diameter criterion of 2 mm. These results suggest that even at a diameter interval of just 0.1 mm, differences between FR growth parameters can be detected and that perhaps the use of a single large diameter class is not appropriate in FR studies. Perhaps the use of diameter classes based on root function, nutrient content, or branching order should be considered in the future.

There were no significant differences in FR biomass between three different MR sampling orientations at the HJP94, OJP, and OA sites, suggesting that the standard practice of collecting root images along the top side of MR tubes is acceptable for determining root biomass and production. Fine root production was found to have similar results with no significant differences between sampling orientations with the exception of OA in July of 2006, where the top was found to be different than the sides. As this study was only conducted for two months, the high levels of variability in the data make it difficult to draw any concrete conclusions, but there appears to be no reason to question MR data collected along the top of the tubes. However, during the physical excavation of several MR tubes at each site, it was noted that approximately two to five roots (not including laterals) had preferentially grown along the length of the tubes on all sides (although not all sides on all tubes) as well as below them. This is likely due to enhanced growing conditions such as increased nutrient and moisture availability as well as decreased resistance to root penetration, which are likely artifacts of tube installation.

Future research is suggested to further develop installation techniques that maximize contact at the soil/tube interface and minimize soil disturbance. Novel methods such as the use of inflatable bladders within the MR tube hole (Gijsman et al., 1991; Volkmar, 1993) and lengths of angle iron driven below the MR tube, forcing it upward to reduce voids at the soil/tube interface (Phillips et al., 2000), have been explored in the past. One possible solution to ensure good soil/tube contact would be the use of a reverse-tapered bit (similar to that used in the installation of tubes in this study) that was slightly smaller (perhaps only 1 mm less) than the diameter of the MR tubes to bore the initial hole. The traditional blunt tube end cap could then be replaced with one of a conical shape. The cone would aid in the insertion of the tube by slightly pushing the soil surrounding the tube outward. If the MR tube was only 1 mm or so larger than the hole, the degree of soil compaction around the tube would be minimal and perhaps retighten the soil loosened during the

coring process. The possible impact of this compaction on root growth would have to be examined.

There are a number of areas of study related to the MR technique itself that should also be addressed in future research. First and foremost is an evaluation of methods of converting raw MR data to actual biomass and productivity. This study used the plane intersect method (PIM) as proposed by Bernier and Robitaille in 2004. Other studies are based on root number or root length/volume with an arbitrary depth of field to calculate root length density (RLD) (Bernier and Robitaille, 2004; Block, 2004; López et al., 2001; Steele et al., 1997). Each method has its own strengths, weaknesses, and assumptions. A thorough comparison of these three methods used on the same data set and not just a literature review would be very helpful.

It has recently been brought to light that the PIM may require further correction (Pierre Bernier, co-developer of the PIM, personal communication). These new scaling factors include correction for roots that are visible in multiple images (image contamination) and roots that have branched within an image (second and third order roots are removed from the analysis). While the removal of higher order roots apparently has little effect on overall production values (reduction of only 2 – 5%), the correction factor for root contamination of an image from outside the measurement area could have a huge impact (corrections of nearly 40%) on productivity estimates. It was not possible to include any of these corrections in this thesis due to time constraints. However, even without any correction, the biomass values measured in this study were comparable to values in the literature as well as those from soil cores from a one-time sampling as discussed in Chapter 3. As productivity is measured as the difference in biomass between two sampling dates, it stands to reason that the productivity values presented in Chapter 3 are also within reason. The results of the one-time soil core comparison to MR biomass values show promise, but would be more valuable if more sampling dates were used.

It is desirable in any study to have as many sampling periods as economically and logistically possible while still being able to detect differences in the parameter being investigated (Tingey et al., 2003). This study had five sample periods per year, beginning with the end of May and continuing monthly until the end of September with calculated values for October representing FR growth parameter estimates for a "winter" period of October to May. As a result of this sampling schedule, no FR biomass or production values were calculated for the month of May. By not capturing FR production values for May (potentially a period of rapid root growth), annual NPP values may be underestimated. To calculate FR biomass and production

values for May, an additional image sampling session would be required at the end of April. As such, it would be prudent to begin MR image collection as soon as possible after the start of the field season for future projects.

One final aspect that this study did not look at was the impact of mycorrhizae on estimates of FR biomass and production. At the jack pine sites in particular, ectomycorrhizae were witnessed in some of the MR images. Fogel (1983) suggested that an additional 8% of total tree biomass could be attributed to mycorrhizae in young Douglas fir (*Pseudotsuga menziesii*) stands. For a 30 year old Douglas fir stand in Michigan, they also reported that 67 – 78% of total FR biomass was from mycorrhizae. This is potentially a very large contribution to total ecosystem C production and biomass. Mycorrhizal roots are believed to be very dynamic with production and mortality occurring simultaneously (Fitter, 1996; Hooker et al., 1995). Majdi et al. (2001) found that mycorrhizal root longevity was strongly related to branching order and soil depth. Hooker et al. (1995) reported that *Populus generosa inter americana* (interamerican hybrid poplar) roots colonized with arbuscular mycorrhizae had a lower longevity than uncolonized roots. However, King et al. (2002) found that longevity increased with mycorrhizal infection for loblolly pine. With approximately 80% of all plants being capable of forming symbiotic relationships with arbuscular mycorrhizae (Hooker et al., 1995), it appears that investigating the influence of mycorrhizae on FR growth parameters in Saskatchewan's boreal forest is an important step that should be taken.

With each passing year, researchers unravel more of the mysteries that lie beneath the forest floor. While there are still many facets of root research left to analyze, tools such as MR make the task less arduous. With further study into the development and implementation of improved methods of converting MR data to discrete values such as root biomass, production, turnover, and longevity, it is possible for scientists to gain better insight into the complexities of root C-cycling. Understanding the dynamics of FR and how they respond to global climate change and fluctuations in atmospheric CO_2 may enable us to predict which forests may be possible C sinks or sources to better monitor land use changes.

6.1 Literature Cited

Bernier, P.Y., and G. Robitaille. 2004. A plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265:165-173.

Block, R.M.A. 2004. Fine root dynamics and carbon sequestration in juvenile hybrid poplar plantations in Saskatchewan, Canada, University of Saskatchewan, Saskatoon, SK.

Dubach, M., and M.P. Russelle. 1995. Reducing the cost of estimating root turnover with horizontally installed minirhizotrons. Agron. J. 87:258-263.

Fitter, A. 1996. Characteristics and functions of root systems, p. 1-20, *In* Y. Waisel, A. Eshel, and U. Kafkafi, ed. Plant roots: the hidden half, 2nd ed. Marcel Dekker, Inc., New York, NY, USA.

Fogel, R. 1983. Root turnover and productivity of coniferous forests. Plant Soil 71:75-85.

Gijsman, A.J., J. Floris, M. Noordwijk, and G. Brouwer. 1991. An inflatable minirhizotron system for root observations with improved soil/tube contact. Plant Soil 134:261-269.

Hooker, J.E., K.E. Black, R.L. Perry, and D. Atkinson. 1995. Arbuscular mycorrhizal fungi induced alteration to root longevity of poplar. Plant Soil 172:327-329.

King, J.S., T.J. Albaugh, H.L. Allen, M. Buford, B.R. Strain, and P. Dougherty. 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154:389-398.

López, B., S. Sabaté, and C.A. Gracia. 2001. Annual and seasonal changes in fine root biomass of a *Quercus* ilex L. forest. Plant Soil 230:125-134.

Majdi, H., E. Damm, and J.-E. Nylund. 2001. Longevity of mycorrhizal roots depends on branching order and nutrient availability. New Phytol. 150:195-202.

Malhi, Y., D.D. Baldocch, and P.G. Jarvis. 1999. The carbon balance of tropical, temperate, and boreal forests. Plant Cell Environ. 22:715-740.

Phillips, D.L., M.G. Johnson, D.T. Tingey, C. Biggart, R.S. Nowak, and J.C. Newsom. 2000. Minirhizotron installation in sandy, rocky soils with minimal soil disturbance. Soil Sci. Soc. Am. J. 64:761-764.

Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17:577-587.

Tingey, D.T., D.L. Phillips, and M.G. Johnson. 2003. Optimizing minirhizotron sample frequency for an evergreen and deciduous tree species. New Phytol. 157:155-161.

Volkmar, K.M. 1993. A comparison of minirhizotron techniques for estimating root length density in soils of different bulk densities. Plant Soil 157:239-245.

APPENDIX A.
SAS script for implementing the plane intersect method

/*This procedure is designed to process minirhizotron data in order to obtain fine root productivity in g of dry mass per m2 of horizontal ground surface. It follows "Method #2" of Bernier and Robitaille, (2004). For any question or comments, please contact Pierre Bernier(pbernier@cfl.forestry.ca)

The first infile is the main fine root data file and is read into TMP. Each line must be a single observation of one particular root at one particular date. This infile must be an EXCEL file and it must have the following column names: Tube, Frame, Root, Date and RtDiam.

Tube, frame and root columns must contain sequential integers only (no letters); Date must be in a Julian or day-of-year format; RtDiam must be in mm.

The second infile contains the tube and site descriptors and is read into TubeProp. It must also be an EXCEL file and have the following column names: Tube, TubeAngle, Slope, StonFrac, as well as parameter values for A0, A1 and A2 for describing the specific mass of the fine roots.

Tube is the tube number as in the first infile. TubeAngle is the angle of the tube (in degrees) with respect to the ground. Slope is the slope angle (in degrees) with respect to the horizontal. StonFrac is the fraction of coarse (D>2mm) particles in the soil (0<=stonFrac<=1). Parameters A0, A1 and A2 describe the specific mass of the roots (in g/cm3).
A0 is an average specific mass.
A0 is given a value >0 only if an average specific mass value is used.
A0 is set to 0 if a diameter-dependant function is used to describe the specific mass of roots
A1 and A2 are the two parameters of a Poisson function "A1*(1-exp(-A2*RootDiam)"
A1 and A2 are adjusted to field data supporting the diameter dependency of specific mass
A1 and A2 are set to 0 if only a mean specific mass (i.e. A0>0) is used

The results are written to an EXCEL file for which the user must provide appropriate directory coordinates in the last procedure of this program. This final output files produces for each observation date (except the first one) and for each tube the following variables:
Mass_T0, Mass_T1 and productivity,
Mass_T1 is the actual mass of roots observed at the date indicated on the line,
Mass_T0 is the mass of roots seen at the previous date (but without those roots that will have disappeared at T2 (see Bernier and Robitaille (2004) for details)). Productivity is the difference between these two numbers. Productivity cannot be a negative value. All masses are given in g/m2 of horizontal ground surface*/

```
PROC IMPORT OUT= Tmp
        DATAFILE= "C:\your directory\your_Root_File.xls"
        DBMS=EXCEL2000 REPLACE;
   GETNAMES=YES;
RUN;
PROC IMPORT OUT= TubeProp
        DATAFILE= "C:\your directory\your_tube_properties.xls"
                                DBMS=EXCEL2000 REPLACE;
   GETNAMES=YES;
RUN;
options linesize=80;
```

```
/****************** START DATA PREPARATION ***********************/
/*Creates file TMP1; creates a specific ID for each observation
that is made up or the root identifiers and the  date*/
DATA Tmp1;
        SET Tmp;
        ID = COMPBL(Tube||Frame||Root);
RUN;
/*Sorts TMP1 by root ID and date*/
PROC SORT DATA = Tmp1;
        BY ID DATE;
RUN;
/*In TMP1, creates three new columns called MaxDiam ADDNEW and DECreasing*/
DATA Tmp1;
        SET Tmp1;
        MaxDiam = RtDiam;
        ADDNEW = '       ';
        DEC = '       ';
RUN;
/*Creates table DATE_ALL that contains the list observation dates*/
PROC SQL;
        CREATE TABLE DATE_ALL AS
                SELECT DISTINCT DATE
                FROM Tmp
                ORDER BY DATE;
/*Creates table Rt_FL that identifies the first and last measurement date for each root*/
        CREATE TABLE Rt_FL AS
                SELECT ID, MIN(DATE) AS DATEF, MAX(DATE) AS DATEL
                FROM Tmp1
                GROUP BY ID
                ORDER BY ID;

/*In Rt_FL, numbers all lines sequentially in the variable "NUM"*/
DATA Rt_FL;
        SET RT_FL;
        Num = _N_;
RUN;
/*Merge Tmp1 and Rt_FL by root ID: this assigns first and last dates to all root
observations*/
PROC SQL;
        CREATE TABLE Tmp1 AS
                SELECT a.*, b.Num
                FROM Tmp1 as a, Rt_fl as b
                WHERE a.ID = b.ID;
/*Counts the number of roots*/
PROC SQL;
        CREATE TABLE NBROOT AS
        SELECT COUNT(*) AS NBROOT
        FROM RT_FL;
/*Calls up macro nbroot using nbroot as input*/
DATA nbRoot;
        SET nbRoot;
```

```
        CALL symput("nbRoot",nbRoot);
RUN;
```
/*This macro checks root by root (unique ID) if there are missing observations within a sequence of observations of a given root, and if diameter of that root is decreasing. If there are missing observations, it adds a new line that contains the same RtDiam as the line above. If the diameter is decreasing, it maintains in column MaxDiam the maximum diameter ever measured for that root. Analysis of productivity will be done using this column. Labels "adding" and "decrease" are added to the temporary file to identify lines that were either added or modified. The macro creates a new file calles "ALL" that contains the following columns: id Date MaxDiam ADDNEW dec. See Bernier and Robitaille (2004) for further explanation on the necessity of this procedure*/

```
%MACRO nbroot;
        /*Loop through all roots*/
        %DO i=1 %TO &nbRoot %BY 1;
                /*Add the root number to the list of dates*/
                DATA date;
                        SET Rt_fl (where = (Num = &i));
                RUN;

                PROC SQL;
                        CREATE TABLE Dates AS
                                SELECT a.*, b.*
                                FROM date AS a, date_All AS b;
                DATA Dates;
                        SET Dates;
                        IF date < datef OR date > datel THEN DELETE;
                RUN;
                DATA root;
                        SET Tmp1 (where = (Num = &i));
                RUN;
                DATA Roots;
                        MERGE Root Dates;
                        BY Date;
                RUN;

                PROC IML;
                        USE roots;
                        READ ALL;
                        matSize = nRow(MaxDiam);
                        row = 1;
                        DO WHILE (row < matSize);
                                MaxDiam_p = MaxDiam[row];
                                id_p = ID[row];
                                Tube_p = Tube[row];
                                row1 = row+1;
                                MaxDiam_n = MaxDiam[row1];
                                IF MaxDiam_n = . THEN DO;
                                        MaxDiam[row1] = MaxDiam_p;
                                        id[row1] = id_p;
                                        Tube[row1] = Tube_p;
```

```
                                        ADDNEW[row1] = 'adding';
                        END;
                        IF (MaxDiam_n < MaxDiam_p & MaxDiam_n > .) THEN
DO;
                                        MaxDiam[row1] = MaxDiam_p;
                                        dec[row1] = 'decrease';
                        END;
                                row = row + 1;
                        END;
                CREATE rep VAR{id Tube Date RtDiam MaxDiam ADDNEW dec};
                        APPEND;
                        CLOSE rep;

                        PROC APPEND BASE=All;
                        RUN;
%END;
%MEND;
%nbroot;
/************************ END DATA PREPARATION **********************/

/************************** START INCREMENT ********************/
/*In this section, fine root productivity is computed as in the Method 2 of Bernier and
Robitaille (2004), using their equations 1, 2 and 3.  The variables are:
rho: the specific mass, g/cm3
alpha: the angle of the tube w/r to the ground , degrees
beta: the angle of the ground with respect to the horizontal, degrees
StonFrac: the fraction of coarse material in the soil
A0 is the average specific mass (g/cm3) if only an average is used
A0 is set to 0 is values are provided for parameters A1 and A2
A1 is the first parameter of a two-parameter Poisson function
A2 is the second parameter of a two-parameter Poisson function
A1 and A2 are set to 0 if a value of A0 is provided

The computation assumes that W, the width of the minirhizotron frames
is equal to 18 mm

This section computes the volume per unit area of ground for each individual root
All the roots are within file "ALL", a file created above in the macro*/

DATA Tubeprop2;
        SET Tubeprop;
        sinAlpha=sin(3.1416*(alpha)/180);
        cosBeta=cos(3.1416*(beta)/180);
RUN;
PROC SQL;
        CREATE TABLE All1 AS
                SELECT a.*, b.sinAlpha, b.cosBeta, b.StonFrac, b.A0, b.A1, b.A2
                FROM All AS a left join Tubeprop2 AS b
                ON a.Tube = b.Tube;
```

```
/* Computes the volume of each root as in eqs 1 and 2 of Bernier and Robitaille (2004). Make sure that the units of Rho, the specific mass, are g/cm3 and that of the root diameters is mm*/

DATA Tmp2;
        SET All1;
        rho = A0+A1*(1-exp(-A2*maxDiam));
        W=18;
        Ae=3.1416**2*(maxDiam/2)**2/sqrt(2);
        P = 2*10**6*(rho/1000)*(1-StonFrac)*Ae * sinAlpha*cosBeta/W;
RUN;
PROC DATASETS;
        DELETE ALL;
RUN;

/*Identifies the last date of measurement in the main file Tmp2 within a new file T2*/

PROC SQL;
        CREATE TABLE T2 AS
                SELECT a.*, b.num
                FROM  Tmp2 as a left join rt_fl as b
                ON a.ID = b.ID AND a.Date = b.Datel;

/*In new file T3_START, for a particular date, selects all roots that are not at their last date of measurement*/

PROC SQL;
        CREATE TABLE T3_START AS
                SELECT Tube, Date, sum(P) as Sum_P
                FROM  T2
                WHERE Num =.
                GROUP BY Tube, DATE
                ORDER BY Tube, DATE;
/*In new file T3_end, for a particular date, selects all roots, even those at
                their last date of measurement*/
        CREATE TABLE T3_END AS
                SELECT Tube, Date, sum(P) as Sum_P
                FROM  T2
                GROUP BY Tube, DATE
                ORDER BY Tube, DATE;
DATA T3_START;
        SET T3_START;
        ID_ = COMPBL(TUBE || DATE);
RUN;
DATA T3_END;
        SET T3_END;
        ID_ = COMPBL(TUBE || DATE);
RUN;
/*Add the volume computed from eq. 2 to T3_START, grouped by date*/
PROC SQL;
        CREATE TABLE T3_START AS
```

```
                    SELECT b.Tube, b.Date, a.Sum_P
                    FROM  T3_START as a RIGHT JOIN T3_END as b
                    ON a.ID_ = b.ID_;
/*Adds a label number*/
DATA T3_START;
        SET T3_START;
        Num = _N_ ;
        IF Sum_P = . THEN Sum_P = 0;
RUN;
/*Labels the end dates sequentially*/
DATA T3_END;
        SET T3_END;
        Num = _N_ - 1;
        IF Sum_P = . THEN Sum_P = 0;
RUN;
/*Creates table "Diff" as the difference in volumes between dates "Start" and "END" and the
resulting change in mass is attributed to the last date of the date pair in "b.date"*/
PROC SQL;
CREATE TABLE Diff AS
                    SELECT b.Tube, b.Date, a.Sum_P AS Mass_t0, b.Sum_P AS Mass_t1,
Mass_t1 - Mass_t0 AS Increment
                    FROM  T3_START as a , T3_END as b
                    WHERE a.Num = b.Num;

/************************** END INCREMENT ************************/
PROC EXPORT DATA= Diff
      OUTFILE= "C:\your directory\OUTPUT.xls"
      DBMS=EXCEL2000 REPLACE;
RUN;
```

APPENDIX B.
Statistical summaries for selected Chapter 3 components

Table B.1 Repeated measures ANOVA for fine root biomass estimates from minirhizotrons at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 showing monthly effects.

Site	Year	Source	df	Mean Square	*F*	*p-value*
HJP94	2003	Month	4	0.138	6.94	0.000*
		Error	32	0.020		
	2004	Month	4	0.043	1.14	0.355
		Error	32	0.038		
	2005	Month	4	0.092	6.89	0.000*
		Error	32	0.013		
	2006	Month	4	0.144	11.2	0.000*
		Error	32	0.013		
OJP	2003	Month	4	4.24	108.0	0.000*
		Error	32	0.039		
	2004	Month	4	0.103	3.54	0.017*
		Error	32	0.029		
	2005	Month	4	0.160	13.2	0.000*
		Error	32	0.012		
	2006	Month	4	0.063	9.20	0.000*
		Error	32	0.007		
OA	2003	Month	4	0.215	5.86	0.001*
		Error	32	0.037		
	2004	Month	4	0.184	5.69	0.001*
		Error	32	0.032		
	2005	Month	4	0.146	15.2	0.000*
		Error	32	0.010		
	2006	Month	4	0.134	7.85	0.000*
		Error	32	0.017		
OBS	2003	Month	4	0.434	17.5	0.000*
		Error	32	0.025		
	2004	Month	4	0.672	7.20	0.000*
		Error	32	0.093		
	2005	Month	4	0.406	47.2	0.000*
		Error	32	0.009		
	2006	Month	4	0.070	4.94	0.003*
		Error	32	0.014		

* denotes significance at $\alpha = 0.1$

Table B.2 Repeated measures ANOVA for fine root production estimates from minirhizotrons at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 showing the effects of months between years, differences between years and the interactions between months and years.

Site	Source	df	Mean Square	*F*	*p-value*
HJP94	Year	3	2.21	1.23	0.315
	Error	24	3.37		
	Month	4	5.71	3.60	0.081*
	Error	32	5.10		
	Year *x* Month	12	1.44	1.17	0.316
	Error	96	1.23		
OJP	Year	3	0.518	1.27	0.307
	Error	24	0.408		
	Month	4	1.38	3.95	0.032*
	Error	32	0.350		
	Year *x* Month	12	1.45	4.22	0.000*
	Error	96	0.344		
OA	Year	3	2.29	6.15	0.024*
	Error	24	0.372		
	Month	4	3.11	12.0	0.000*
	Error	32	0.260		
	Year *x* Month	12	0.875	3.51	0.000*
	Error	96	0.249		
OBS	Year	3	1.33	1.52	0.236
	Error	24	0.876		
	Month	4	4.17	6.04	0.001*
	Error	32	0.690		
	Year *x* Month	12	0.252	0.856	0.593
	Error	96	0.613		

* denotes significance at $\alpha = 0.1$

Table B.3 Repeated measures ANOVA for fine root production estimates from minirhizotrons at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006 showing monthly effects.

Site	Year	Source	df	Mean Square	*F*	*p-value*
HJP94	2003	Month	4	5.78	1.92	0.131
		Error	32	3.01		
	2004	Month	4	0.273	0.983	0.431
		Error	32	0.278		
	2005	Month	4	3.87	1.99	0.120
		Error	32	1.95		
	2006	Month	4	0.113	2.18	0.093*
		Error	32	0.052		
OJP	2003	Month	4	3.96	7.56	0.000*
		Error	32	0.523		
	2004	Month	4	0.212	0.918	0.465
		Error	32	0.231		
	2005	Month	4	1.27	2.84	0.040*
		Error	32	0.446		
	2006	Month	4	0.295	1.63	0.190
		Error	32	0.181		
OA	2003	Month	4	3.00	10.0	0.000*
		Error	32	0.300		
	2004	Month	4	1.40	4.92	0.003*
		Error	32	0.285		
	2005	Month	4	0.193	1.70	0.174
		Error	32	0.113		
	2006	Month	4	1.14	3.68	0.014*
		Error	32	0.309		
OBS	2003	Month	4	3.13	2.07	0.108
		Error	32	1.51		
	2004	Month	4	1.18	4.47	0.006*
		Error	32	0.264		
	2005	Month	4	1.06	1.76	0.162
		Error	32	0.602		
	2006	Month	4	0.373	2.435	0.067*
		Error	32	0.153		

* denotes significance at $\alpha = 0.1$

Table B.4: Paired-means t-tests for fine root biomass estimates from minirhizotrons and soil cores to a vertical depth of 35 cm at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for August 2005.

Site	Mean Difference	df	*t*	Sig. (2-tailed)	*r*
HJP94	-1.31	8	-4.00	0.004*	0.816
OJP	-0.938	8	-0.326	0.753	0.115
OA	0.0685	8	0.267	0.796	0.0940
OBS	-0.212	8	-0.458	0.659	0.160

* denotes significance at $\alpha = 0.1$

APPENDIX C.
Soil moisture and soil temperature data for 2003 to 2006

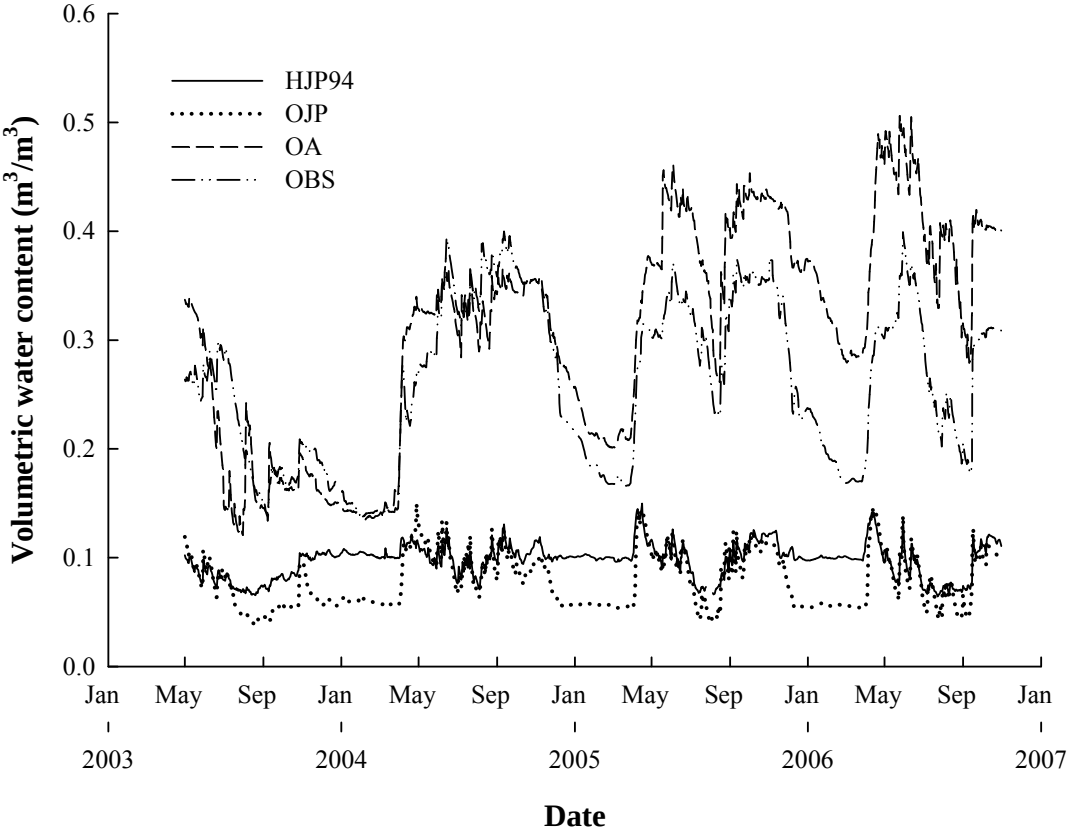

Figure C.1: Daily mean soil volumetric water content (VWC) for HJP94, OJP, OA, and OBS for 2003 to 2006 for a depth interval of 0 – 60 cm (Fluxnet Canada, DIS, 2008).

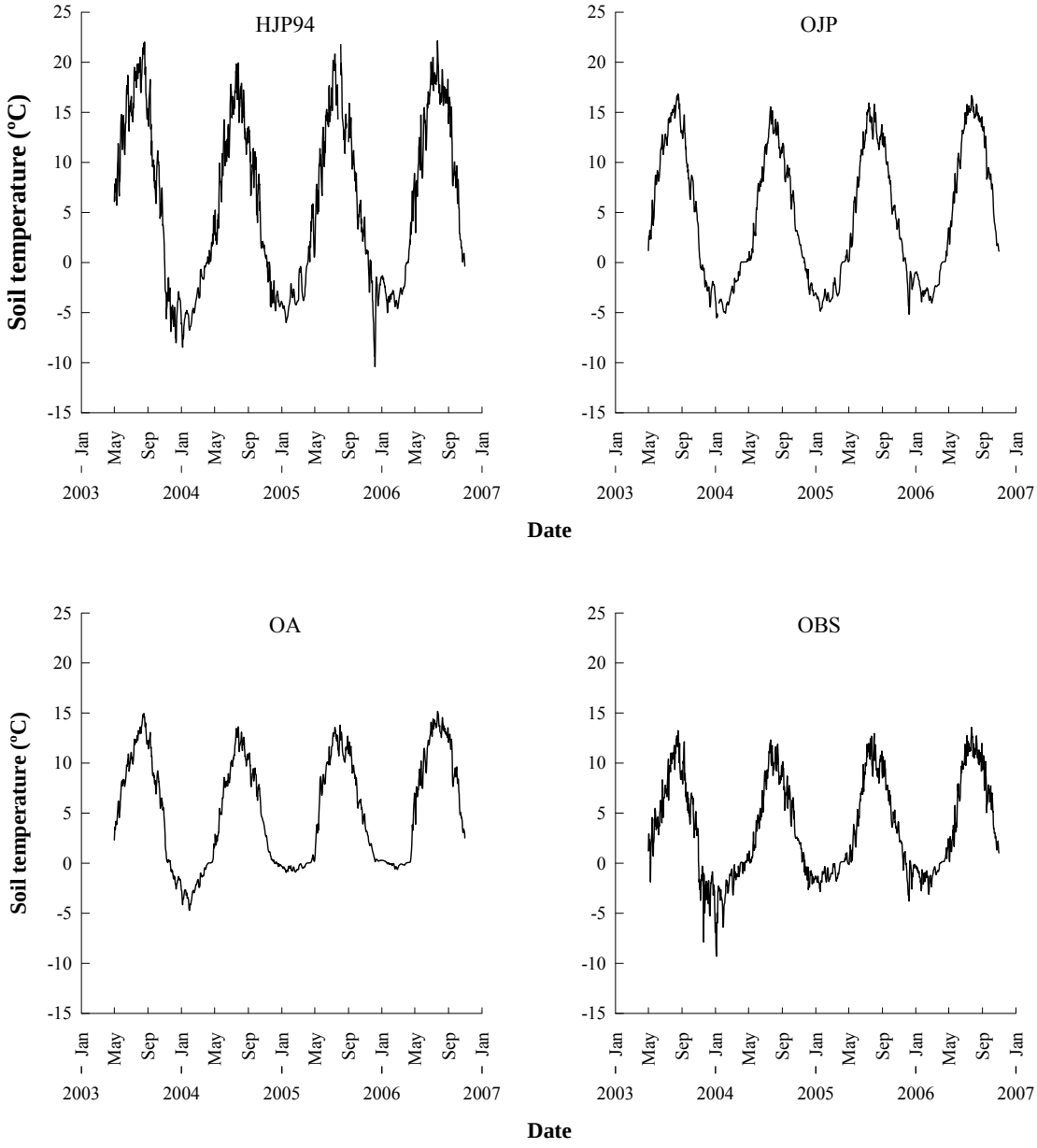

Figure C.2: Daily mean soil temperatures for HJP94, OJP, OA, and OBS for 2003 to 2006 for a depth interval of 0 – 50 cm (Fluxnet Canada, DIS, 2008).

APPENDIX D.
Statistical summaries for selected Chapter 4 components

Table D.1: One-way ANOVAs for mean annual fine root biomass, production, turnover, and longevity estimates from minirhizotrons for three depth ranges at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan for 2003 to 2006.

Parameter	Site	Depth (cm)	df	Mean Square	*F*	*p-value*
FR Biomass	HJP	0 – 40	4	2.17	57.7	0.000*
		0 – 20	4	0.555	1.32	0.299
		20 – 40	4	0.252	1.59	0.216
	OJP	0 – 40	4	1.23	43.8	0.000*
		0 – 20	4	0.358	1.30	0.308
		20 – 40	4	0.118	1.33	0.303
	OA	0 – 40	4	0.541	42.0	0.000*
		0 – 20	4	0.103	1.11	0.391
		20 – 40	4	0.286	1.55	0.237
	OBS	0 – 40	4	0.848	19.0	0.000*
		0 – 20	4	0.311	1.76	0.171
		20 – 40	4	0.104	0.675	0.649
FR Production	HJP	0 – 40	4	0.007	0.508	0.767
		0 – 20	4	0.003	0.392	0.848
		20 – 40	4	0.001	0.475	0.790
	OJP	0 – 40	4	0.021	0.970	0.462
		0 – 20	4	0.015	0.963	0.466
		20 – 40	4	0.001	0.921	0.490
	OA	0 – 40	4	0.007	1.59	0.213
		0 – 20	4	0.002	1.28	0.316
		20 – 40	4	0.002	1.00	0.444
	OBS	0 – 40	4	0.008	0.731	0.610
		0 – 20	4	0.008	0.908	0.498
		20 – 40	4	0.002	0.397	0.844
FR Turnover	HJP	0 – 40	4	0.109	0.952	0.472
		0 – 20	4	0.053	0.95	0.473
		20 – 40	4	0.145	1.56	0.221
	OJP	0 – 40	4	0.087	3.11	0.034*
		0 – 20	4	0.071	1.59	0.213
		20 – 40	4	0.09	1.41	0.228
	OA	0 – 40	4	0.362	2.24	0.094*
		0 – 20	4	0.417	4.29	0.010*
		20 – 40	4	0.006	0.583	0.680
	OBS	0 – 40	4	0.154	1.07	0.411
		0 – 20	4	0.168	1.42	0.263
		20 – 40	4	0.143	0.954	0.46
FR Longevity	HJP	0 – 40	4	1.79	0.788	0.573
		0 – 20	4	0.825	0.504	0.734
		20 – 40	4	13.3	2.80	0.048*
	OJP	0 – 40	4	9.29	1.61	0.210
		0 – 20	4	3.06	1.62	0.211
		20 – 40	4	67.8	0.639	0.607
	OA	0 – 40	4	147	3.89	0.014*
		0 – 20	4	25.7	4.67	0.009*
		20 – 40	4	170	0.837	0.523
	OBS	0 – 40	4	0.836	0.711	0.624

* denotes significance at $\alpha = 0.1$

APPENDIX E.
Statistical summaries for selected Chapter 5 components

Table E.1: One-way ANOVAs for mean annual fine root biomass and production, from minirhizotrons for two months in 2006 at four boreal forest sites (HJP94, OJP, OA, and OBS) in northern Saskatchewan.

Site	Month	df	Mean Square	*F*	*p-value*
	Fine root biomass				
HJP94	July	2	0.174	0.300	0.752
	August	2	0.187	0.319	0.738
OJP	July	2	0.244	0.982	0.428
	August	2	0.263	1.04	0.409
OA	July	2	0.425	1.96	0.235
	August	2	0.328	1.26	0.361
	Fine root production				
HJP94	July	2	0.041	0.104	0.903
	August	2	0.051	1.98	0.218
OJP	July	2	0.054	0.609	0.574
	August	2	0.102	0.818	0.485
OA	July	2	0.218	5.19	0.060*
	August	2	0.031	0.255	0.784

* denotes significance at $\alpha = 0.1$